Structure, composition and dynamics of *Metrosideros excelsa* (pōhutukawa) forest, Bay of Plenty, New Zealand

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Abstract

The structure, composition and dynamics of a rare forest type, *Metrosideros excelsa* (henceforward referred to as *Metrosideros*) forest, were assessed in the Bay of Plenty Region, North Island, New Zealand. *Metrosideros* and associated species' shade tolerances were also investigated. Study sites extended from Waihi Beach in the west, to Opape headlands in the east of the region. Thirty five quadrats ranging from 50–400 m^2 in size were measured resulting in a total survey area of 14,200 m^2.

Metrosideros forests were floristically poor in comparison to other indigenous forest types; though semi-coastal *Metrosideros* forest hosted a more diverse understory than coastal forest. A total of 122 indigenous species were recorded, however only a minority of these were considered common and widespread, such species included *Coprosma macrocarpa*, *Coprosma robusta*, *Cyathea dealbata*, *Melicytus ramiflorus*, *Myrsine australis*, *Pseudopanax lessonii*, *Pseudopanax arboreus*, *Beilschmiedia tawa*, *Dysoxylum spectabile* and *Litsea calicaris*. In general, forest understories comprised of a sparse shrub layer, overtopped by a sub-canopy dominated by either tree ferns in steep inland localities, *Pseudopanax* spp., *Coprosma* spp. and *Melicytus ramiflorus* on coastal headlands, or *Coprosma* spp., *Myrsine*, *Beilschmiedia*, *Dysoxylum* and *Litsea* in mature and semi-coastal forest.

Metrosideros growth rates were determined in two ways; first from the diameter growth of stems in four permanent quadrats, and second from ring counts on cut stem disks. *Metrosideros* stems initially had high growth rates, which could exceed 4 mm $year^{-1}$ in the first 80 years, however diameter growth subsequently slowed down as trees developed. All *Metrosideros* populations had regenerated in cohorts. The derived diameter age relationship suggested that stands ranged from 20–>300 years old, with mature forest being formed within 250 years. The oldest trees measured may be >1000 years old, and represent relics of the regions original vegetation.

The sequence of forest development quantified for Bay of Plenty forests shows a decline in *Metrosideros* stems from >2000–<400 stems ha^{-1} over a period of c. 300 years; a result of self-thinning. This was coupled with an increase in

Metrosideros basal area from <20 m^2 ha^{-1} to an average of 50 m^2 ha^{-1}; plateauing after 70 years. Total stem density and basal area were greatest in stands between 60–300 years old.

The diameter frequency distributions quantified for key species suggested that appreciable shifts in species composition were occurring. The replacement strategies among key canopy species involved establishment at different phases of forest development, and this directly reflected species' differing shade tolerances. Shade intolerant species *Metrosideros* and *Kunzea ericoides* (which could form mixed stands) established solely following disturbance. *Metrosideros* forest is likely to replace itself indefinitely on the unstable coastal headlands cliffs in the region, where frequent disturbances provide suitable regeneration sites. However, in semi-coastal localities, where disturbance is less frequent, *Metrosideros* is succeeded by shade tolerant species. *Litsea*, *Dysoxylum* and *Corynocarpus laevigatus* establish in mid-successional forest, however may be somewhat reliant on canopy gaps to stimulate height growth. Conversely *Beilschmiedia*, the most shade tolerant species, commonly establishes in mature forest and is capable of continued regeneration; thus is likely to be a dominant component of the forest community that replaces *Metrosideros* forest, in the Bay of Plenty.

This research contributes to the national reporting of quantitative data describing the structure and composition of New Zealand's indigenous forests, provides the first quantitative model of forest succession in *Metrosideros* forest in the Bay of Plenty, and contributes to the understanding of linkages between species' shade tolerance, regenerative strategies and successional status.

Key words: *Metrosideros excelsa***,** pōhutukawa, *Litsea calicaris***,** *Beilschmiedia tawa*, coastal forest, dynamics, composition, structure, succession, shade tolerance, diameter growth rates, Bay of Plenty.

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Chapter One: Introduction

This research addresses the current lack of demographic data and knowledge of the successional trends occurring within *Metrosideros excelsa** forests. The Bay of Plenty is the chosen setting for this research as the region hosts a number of ecologically significant *Metrosideros* stands, and provides an opportunity to compare and contrast mainland forests with those on offshore islands. This chapter provides background information on *Metrosideros*, outlines the research objectives and provides an overview of the thesis layout.

1.1 *Metrosideros excelsa*

Metrosideros excelsa or pōhutukawa is probably the most well-known and iconic plant species in New Zealand; having significance in both Māori and European culture. The species is renowned for its sudden and spectacular mass flowering episodes, its gnarly and sprawling growth form, and its ability to survive in the most precarious and seemingly inhospitable environments. The brilliant red flowers not only hold a special place in the hearts of New Zealanders, but they are also biologically important; providing a food source to our native nectar feeders, such as the tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*), stitchbird (*Notiomystis cincta*), short-tailed bat (*Mystacina tuberulata*) and native bees (*Hylaeus* spp., *Leioproctus* spp., *Lasioglossum* spp.).

Metrosideros was formerly an important resource to Māori and early European settlers; having many cultural and medicinal uses. Māori regard *Metrosideros* as *rākau rangatira*, a chiefly tree, symbolizing power and authority, and often planted individual specimens to mark prominent and sacred sites (Bergin & Hosking 2006). The word *Metrosideros* is derived from the Greek terms *metra* meaning core or heart, and *sideron* meaning iron, thus *Metrosideros* have been termed "New Zealand's iron hearted trees", a reference to the extreme hardness of their red coloured wood. Not surprisingly, the hard timber was extensively used by early European settlers for construction and boat building, and large quantities of the timber were also exported. Consequently, *Metrosideros* forests soon became a diminishing resource on the mainland (Bergin & Hosking 2006).

*Species nomenclature follows New Zealand Plant Conservation Network (NZPCN 2012)

1.1.1 Distribution and range

Metrosideros is a coastal tree species, native to the warm-temperate region of New Zealand that lies between the Three Kings Islands and latitude 39^{o} S (Wardle 1991). The precise southern limit of natural *Metrosideros* is difficult to establish as the species has been widely transplanted by Māori (Bercusson & Torrence 1998; Bergin & Hosking 2006). *Metrosideros* forest once formed an almost continuous belt around New Zealand's northern coastline; spanning from Urenui on the west coast to possibly Gisborne on the east coast. Natural inland populations also occur in the Rotorua Region; including the Okataina, Rotoiti and Tarawera lake flanks, and the Tarawera River margins (Clarkson et al. 1991). It is speculated that *Metrosideros* forest was much more widespread at inland localities, as a coloniser of lava flows from the Okataina Volcanic Centre. However has since been succeeded by other broadleaf species (Clarkson et al. 1991).

As a result of forest clearance and the adverse effects of browsing mammals, a mere 10% of the original *Metrosideros* forest currently remains (Forest Research Institute 1989). The southern limits have diminished several kilometres northwards to Waiiti beach and Mawhai Point on the west and east coasts respectively. *Metrosideros* forest that remains is highly fragmented, and in many places reduced to isolated forest patches and scattered individual trees (Simpson 2005),

1.1.2 Threats and conservation

Logging, fires and land clearance all contributed to the removal of c. 90% of the original *Metrosideros* forest, much of which occurred in the 1900s. Remaining stands were severely depleted, often reduced to small fragmented stands, showed continued deterioration and lacked ample regeneration sites (Forest Research Institute 1989). This prompted a movement towards the conservation and management of *Metrosideros* forests, predominantly led by the Project Crimson Trust, founded in 1990. The trust manages a sponsorship program dedicated to the protection and enhancement of *Metrosideros* forests and supports large scale community based plantings and protection programs. However, despite the species popularity and the many successes of Project Crimson, *Metrosideros* forests are still under threat, particularly stands without active conservation

management. Current threats include possum/herbivore browse, trampling by stock, genetic pollution and habitat loss due to land development and burning (Hosking 2000).

1.1.3 Ecological characteristics and succession

Metrosideros is an ecological opportunist, tuned in to stochastic disturbance events. Following mass flowering episodes in December–January, trees produce a vast number of tiny wind dispersed seed (Bergin & Hosking 2006). Owing to their small size, seeds only require light winds in the range of 5–19 km per hour to be lofted and dispersed over extremely long distances (Wright et al. 2000). Seed does not persist in the seed bank, and only has a germination window of approximately one year. This dispersal strategy can be considered wasteful but effective, as although much of the seed will fail to germinate, the chance that seed will be dispersed to an ideal germination site is maximised (Schmidt-Adam et al. 1999).

Metrosideros is an early pioneer species, capable of colonising a range of open sites including unstable river margins, exposed coastal cliffs and vertical faces. Like many other species in the genus, *Metrosideros* has a particular affinity for volcanic substrates. However, *Metrosideros* is extremely long lived, with some individuals exceeding 1000 years (Chapter Four). Such longevity is an unusual strategy for a pioneering species.

Where disturbances are frequent, such as on coastal cliffs and headlands, *Metrosideros* forest is capable of a cyclic succession; continually replacing itself (Simpson 2005). Though, in stable environments, once established on the landscape, *Metrosideros* may dominate forest composition for hundreds of years (Atkinson 1994). A combination of persistent leaf litter and a dense canopy slows the invasion of later successional species, and also prevents *Metrosideros* from regenerating beneath itself. However, a suite of shade tolerant species will eventually establish and replace *Metrosideros* in the canopy. Atkinson (2004) has identified *Litsea calicaris*, *Beilschmiedia tawa*, *Beilschmiedia tarairi* and *Dysoxylum spectabile* as mid-late successional species in *Metrosideros* and *Kunzea* forests on New Zealand's northern offshore islands. It is likely a similar suite of species will succeed *Metrosideros* forests in the Bay of Plenty. A more comprehensive review of *Metrosideros* is provided in Chapter Seven, in the format of the New Zealand Biological Flora Series.

1.2 Research objective and aims

The objective of this research is to enhance the current understanding of developmental and successional processes within *Metrosideros* forest in the Bay of Plenty Region. This will aid with the future conservation and management of the species. This thesis contains two main field research components, first a quantitative vegetation survey of *Metrosideros* forest, and second the determination of interspecific shade tolerance variations between *Metrosideros* and later successional species. The following broad research aims are addressed:

(1) Quantification of *Metrosideros* forest structure and composition in the Bay of Plenty Region;

(2) Quantification of *Metrosideros* growth rates and *Metrosideros* and key species' juvenile light requirements;

(3) Development of a successional model for *Metrosideros* forests in the Bay of Plenty, and assess whether, or to what extent, shade tolerance variation between key species drives forest succession.

1.3 Thesis structure

Results from this research are presented in seven chapters including a comprehensive literature review on *Metrosideros excelsa* and a synthesis discussing the findings and significance of this research in a national context.

Chapter One: Background

This chapter provides background information on *Metrosideros excelsa* forests and outlines the research aims.

Chapter Two: Region and study sites

This chapter provides a broad description of the Bay of Plenty Region; the land, the climate and the past and current forest extent. General descriptions and localities of study sites are also provided.

Chapter Three: Forest composition and structure

This chapter utilises data from the comprehensive vegetation survey and reports on *Metrosideros excelsa* forest composition and structure.

Chapter Four: Autecology of *Metrosideros excelsa* and key forest associates

This chapter examines key life history traits of *Metrosideros excelsa* and associated species, particularly juveniles' shade tolerance variations.

Chapter Five: Succession

This chapter combines vegetation survey data, growth rate data and shade tolerance data to report on population structure, regenerative processes and forest succession.

Chapter Six: Biological flora of *Metrosideros excelsa*

This chapter comprises a comprehensive review of current literature available on *Metrosideros excelsa* and incorporates the finding from the present research. It has been prepared in the format of the New Zealand Biological Flora Series (e.g. Bryan et al. 2011).

Chapter Seven: Synthesis

This chapter provides a summary of findings from all previous chapters and assesses their significance in a national context. Recommendations are given for further research.

Chapter Two: Study region and research sites

2.1.1 Coastal forest extent and modification

Prior to human settlement, the Bay of Plenty region was predominantly covered in forest, with the exception of non-forest vegetation types present on mountainous peaks, exposed coastal cliffs, wetlands, estuaries and dunelands. It is likely that *Metrosideros*, *Dysoxylum spectabile*, *Beilschmiedia tawa* and *Vitex lucens* would have dominated forests in the narrow coastal zone. Away from the coast, on inland ridges, these species would have been replaced by *Nothofagus truncata*, *Phyllocl1adus trichomanoides* and *Knightia excelsa*, whilst on hillslopes and gullies, *Beilschmiedia tawa*, *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* would have dominated (Clarkson & Regnier 1989).

The Bay of Plenty coastal zone has a long history of forest disturbance and human induced modification. Settlement began as early as AD 1125 in the region and was focussed in the coastal and lowland zones. Māori cleared extensive areas of forest along the coast, behind Tauranga and Ohiwa harbours and the regions river margins; primarily for cultivation and living space (Phillips, undated). The 19th century arrival of Europeans amplified the demand for productive land, thus the extent and degree of forest disturbance continued to increase and encroached further inland. Virgin forest was cleared for farming, which became the major land use in the area, and remaining forest was modified by excessive logging for firewood and building materials (Rasch 1989; Simpson 2005). Attempts were made to farm much of the rugged hill country eastwards of Whakatane, however these were largely unsuccessful and the majority of farms were abandoned by the 1930s. Consequently, this land has reverted back to regenerating *Kunzea ericoides* and *Leptospermum scoparium* scrublands (Clarkson & Regnier 1989).

It has been estimated that a mere 0.5% of coastal vegetation extending from Ohiwa Harbour to Hicks Bay is protected in scenic reserves or similar. These protected areas are small, highly modified and primarily secondary forest fragments (Clarkson & Regnier 1989; Rash 1989). The proportion of coastal vegetation in managed reserves in the eastern Bay of Plenty is much larger, and is likely to be around 30% of the original area; owing to the presence of larger reserves e.g. Ohope, Kohi Point and Orokawa Scenic Reserves (Beadel & Shaw 1988).

Species commonly referred to throughout this thesis, *Metrosideros excelsa*, *Dysoxylum spectabile*, *Beilschmiedia tawa*, *Vitex lucens*, *Nothofagus truncata*, *Phyllocladus trichomanoides*, *Knightia excelsa*, *Litsea calicaris*, *Leptospermum scoparium*, *Myrsine australis*, *Geniostoma rupestre*, *Melicytus ramiflorus*, *Corynocarpus laevigatus*, *Weinmannia racemosa* and *Hedycarya aborea*, are henceforth referred to by genus name only.

2.2 Regional description

2.2.1 Climate

The Bay of Plenty has a sub-tropical climate with warm humid summers and mild winters; the climate ranges from warm temperate, in the frost free zone adjoining the coast, to sub-alpine on the higher peaks. Summer daytime maximum air temperatures range from 22–26 °C, but seldom exceed 30 °C. Winter has higher rainfalls and unsettled weather. Winter day time temperatures range from 9–16 °C, and although the entire region is within 30 km of the coast, inland valley floors are subject to heavy winter frosts due to cold air drainage and entrapment (Clarkson & Regnier 1989). South-westerly winds from the Pacific Ocean prevail for much of the year. Sea breezes often occur on warm summer days. In summer and autumn, storms of tropical origin may bring extreme winds and heavy rainfall from the east or northeast. Rainfall is less than 1300 mm per annum along the coast, and generally between 1400–1600 mm per annum over the remainder of the region. However, rainfall can exceed 2000 mm in the inland high country. The region is also prone to severe summer droughts; these occur every few years have a strong influence on the regions vegetation (Beadel & Shaw 1988; Clarkson & Regnier 1989).

2.2.2 Physiology and geology

Most of the region from Waihi Beach to Opotiki is composed of low lying hills underlain by Jurassic and Lower Cretaceous greywacke. West of Opotiki the landscape is typified by widely incised valleys and mountainous regions composed of Mesozoic sandstones and siltstones. Sand dunes (many of which have been degraded by development) line the coast from Waihi to Opape, and are broken only by occasional river and harbour mouths, volcanic landforms, and rocky headlands. Harbours and estuaries are a feature of the landscape, with

Tauranga harbour being the most extensive. Low coastal hills and headlands surround both the Tauranga and Ohiwa Harbours. Low lying hills also adjoin the coast between Pukehina and Matata, and a series of coastal cliffs extend from west of Ohiwa Harbour to meet greywacke headlands centred on Kohi Point (Beadel & Shaw 1988; Clarkson & Regnier 1989).

There are four relatively large islands in the Bay of Plenty Region. These are Tuhua (Mayor Island), Moutohora (Whale Island), Whakaari (White Island) and Motiti Island. Several smaller islands and stacks are also present. Islands are all of volcanic origin, with Whakaari currently active, and geothermal activity occurring on Moutohora (Law 2008).

2.2.3 Soils

Soils types in the region vary markedly depending on the landform, parent material and local conditions. Broadly soils on the regions flood plains and valley floors are of recent origin; their development owing to the accumulation of volcanic tephras and/or greywacke alluvium. Soils on the hill country have primarily formed from volcanic tephras. Kaharoa Ash is the dominant soil forming tephra near Waihi Beach and extending eastwards to Te Puke, giving rise to yellow-brown loams. Soils in the region between Te Puke and Ohiwa Harbour have developed upon the Tarawera Ash and Lapilli, giving rise to yellow-brown pumice soils near the coast and yellow-brown pumice to podzolised yellow-brown pumice on steep-lands (between Whakatane and Ohiwa Harbour). Soils eastwards of Ohiwa Harbour have been largely influenced by the Taupo Pumice formation. Eastwards of Opotiki, steep-land soils are predominantly derived from weathering of underlying sedimentary sand and siltstones. Localised soils formed upon thin undifferentiated tephras are also present (Beadel & Shaw 1988; Clarkson & Regnier 1989; Molloy 2003). Coastal soils are within the thermic soil temperature zone; that is their average temperature ranges from c. 10–30 °C (Molloy 2003).

2.3 Current extent of *Metrosideros excelsa* forest

Examples of original *Metrosideros* forest still remain on the coastal slopes and headlands in the Bay of Plenty region. A thin continuous band of *Metrosideros* forest extends from Ohiwa Harbour to well past Te Kaha, breaking only for sandy/gravely beaches and bays (Bergin & Hosking 2006). However, only a small

number of larger intact remnant forests remain, such as that in the Ohope, Orokawa and Matata Scenic Reserves. However these forests suffer from the effects of browsing mammals (possums, goats, deer, and domesticated stock) and pest plant invasion. *Metrosideros* forest is absent from many of the sandy beaches in the Western Bay of Plenty, however it is the dominant coastal species on/around the headlands around Mount Maunganui (Mauao) and nearby islands. Disturbance and human induced modification on the mainland render offshore islands the best examples of intact *Metrosideros* forest, with native plant and animal associates. Both island and mainland sites have been included in this study; site localities are shown on Figure 2.1.

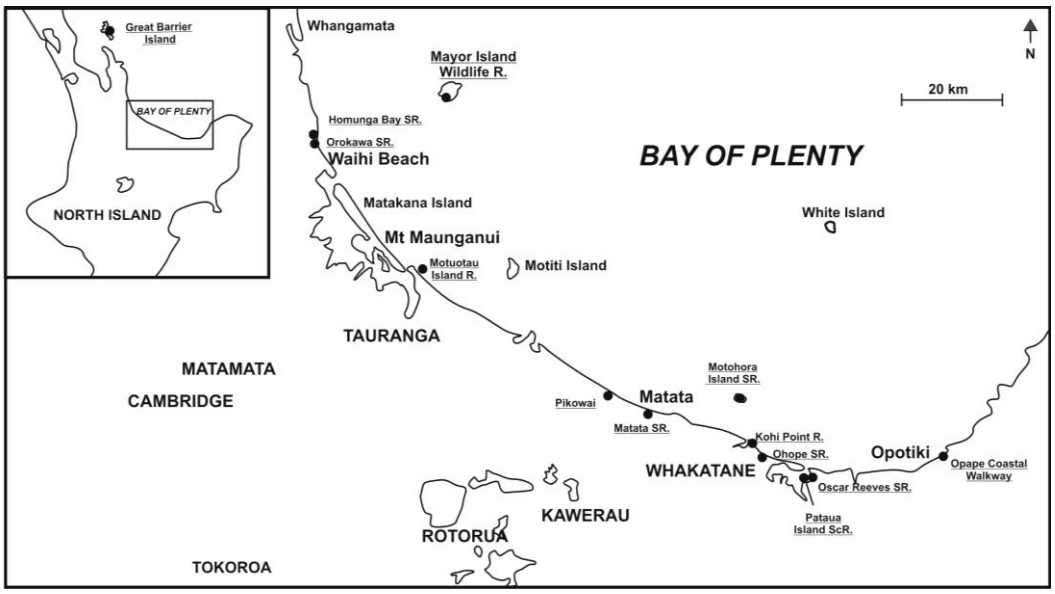


Figure 2.1: Map showing the location of study sites within the Bay of Plenty. Black dots indicate study sites. R= Reserve, SR= Scenic Reserve, Sci R= Scientific Reserve.

2.4 Study site descriptions

2.4.1 Orokawa–Homunga Bay Scenic Reserve

This reserve covers 486 ha and is predominantly vegetated in *Metrosideros*–broadleaved forest; and considered the best remaining example of coastal *Metrosideros* forest in the Waihi Ecological District. The landscape is composed of a narrow band of steep hill country and bounded by steep ignimbrite cliffs on the seaward margin. Vegetation has been extensively modified by anthropogenic disturbances. Originally, *Metrosideros*, *Beilschmiedia*, *Vitex*, *Dysoxylum*, *Kunzea*, *Litsea* and *Corynocarpus* dominated the coastal forest zone. However most of these species have since been cleared from their former forest cover (Wildland Consultants 2006). Currently, *Metrosideros* dominates the reserve with *Vitex* replacing *Metrosideros* inland. Possum and stock browse is evident in the area, with possum numbers having increased by 15% between 2003 and 2007 (Environment Bay of Plenty 2009).

2.4.2 Tuhua (Mayor Island) Wildlife Sanctuary

Tuhua is an approximately circular (5 km diameter) cliff bound island, situated 27 km east of the Coromandel Peninsula. The island is 1277 ha in extent and is predominantly vegetated in coastal (*Knightia*) *Metrosideros*–broadleaved forest. The island comprises the emergent summit of a rhyolitic volcano; a caldera formation is present on the south-western side, creating swampland and lake environments. At present the island is mostly covered with *Metrosideros* forest, but this has undergone rapid change in recent times. Atkinson & Percy (1955) mapped vegetation on the island, and showed amongst the *Metrosideros* dominated headlands and valleys there were also significant areas of *Kunzea*, particularly in the crater zone; these regions have since also become dominated by *Metrosideros* forest. The current *Metrosideros* forest is of post-Polynesian origin. Pollen analysis of swamp sediments have suggested forest was once dominated by *Dacrydium cupressinum* and *Agathis australis*. Polynesian burning (450 years BP) is likely to have cleared these species from their former dominance and initiated the current *Metrosideros* forest succession (Empson et al. 2002). Tuhua is considered a nationally significant site because it is free of possums and other introduced mammals.

2.4.3 Motuotau (Rabbit Island) Reserve

Motuotau is a small 2.6 ha volcanic remnant, situated north east of Mount Maunganui and approximately 500 meters off shore. Native vegetation covers more than 95% of the island and includes coastal *Metrosideros* forest, shrub-fernland and cliff vegetation. Evidence of Māori occupation exists in the form of a pa site and terraces and pits on the island summit and it is likely the current forest developed following disturbance and land clearance associated with Māori occupation (Clarkson & Spring-Rice 1992).

2.4.4 Matata Scenic Reserve

Matata Scenic Reserve is 500 ha in extent, with 140 ha located within the coastal zone. The reserve is situated in the eastern Bay of Plenty and encompasses stream dissected ignimbrite cliffs and steep hill country. Vegetation is predominantly coastal *Metrosideros*/*Kunzea*–broadleaved forest. *Nothofagus* becomes more common inland where it represents the largest remaining example of coastal *Nothofagus–Metrosideros* forest in New Zealand. The reserve was formerly part of a much larger tract of forest extending west to Pongakawa and inland to the lakes of the Rotorua Region. Land clearance has reduced this to a series of small remnants, of which Matata Scenic Reserve is the largest. Vegetation comprises remnant coastal forest (dominants: *Metrosideros*, *Nothfagus*, *Kunzea*, *Dysoxylum*), and secondary forest and shrublands (dominants: *Kunzea*, *Knightia*, *Cyathea medullaris* and *Leucopogon fasciculatus*). The secondary forest is a consequence of logging c. 100 years ago (Wildland Consultants 2006). Landslides and debris flows are a common feature of the area, predominantly caused by high rainfall and loosely consolidated sediments, and these have shaped vegetation in recent times. Severe debris flows occurred in 2005 which scoured much of the Awataraiki and Waitepuru stream channels back to bedrock, widening the channels and removing streamside vegetation (McSaveney et al. 2005). This has provided primary surfaces suitable for *Metrosideros* regeneration (Chapter Three).

2.4.5 Kohi Point Scenic Reserve

Kohi Point Scenic Reserve comprises 168 ha of secondary coastal *Metrosideros*-broadleaved forest and fernland. This reserve is situated upon coastal cliffs and rugged greywacke headlands in the eastern Bay of Plenty, Whakatane. Kohi Point vegetation has been burnt, perhaps repeatedly, over the past two decades and is

now dominated by secondary forest and wind shorn scrublands (Wildland Consultants 2006). Landslides are frequent in the area. Dominant species include *Metrosideros* on the headlands and steep gully sides, with *Knightia* (emergent), *Kunzea, Pseudopanax arboreus* and scattered *Litsea* becoming more dominant inland. Few relict trees remain, predominantly in gullies and these are a markedly larger size compared to secondary forest trees. *Litsea* die back is extensive in this reserve (Environment Bay of Plenty 2009).

2.4.6 Ohope Scenic Reserve

Ohope Scenic Reserve covers 495 ha and is located in the Eastern Bay of Plenty, just south of the Ohope township. The reserve forms part of a significant coastal landscape; adjoining the Mokoroa Bush Scenic Reserve (inland), Ohope pōhutukawa remnants, and is within a few hundred metres of the Kohi Point Scenic Reserve (above). Vegetation is predominantly regenerating coastal/semi coastal *Metrosideros* forest, replaced by *Beilschmiedia–Weinmannia* forest, inland. Ohope Scenic Reserve supports one of the best examples of mature *Metrosideros* forest on the mainland, along with a number of other forest types (Rasch 1989). Intensive possum control has been undertaken so canopy damage from possum browse is minimal (Environment Bay of Plenty 2009).

2.4.7 Oscar Reeves Scenic Reserve

This is a small 6 ha reserve located within a steep gully, situated less than one kilometre from Ohiwa Harbour. Vegetation is secondary forest and is comprised of a mosaic of canopy species, such as *Metrosideros*, *Vitex*, *Knightia*, *Beilschmiedia* and *Dysoxylum*. *Metrosideros* trees are found primarily on ridge tops and cliff faces, *Vitex*, *Knightia*, *Beilschmiedia* and *Weinmannia* dominate the south facing cliffs, with *Acacia mearnsii* and *Paraserianthes lophantha* invading the north facing slopes (both species are prolific in the wider Ohiwa Harbour area). A swampy area hosting a mixture of reed and sedge lands is also present at the bottom of the main gully (Clarkson & Regnier 1989).

2.4.8 Moutohora (Whale Island) Scenic Reserve

Moutohora is a 143 ha dormant volcano, situated 10 km offshore of Whakatane, within the Taupo-Whakaari marine depression. The island is heavily eroded and currently two peaks remain, with the largest rising to 348 m asl. Moutohora was

acquired by the Crown in 1984, and is now managed as a Wildlife Management Reserve (Smale & Owen 1990). Regenerating coastal *Metrosideros*–broadleaved forest is currently the dominant vegetation type, with areas of *Kunzea* scrubland and grasslands also present. The vegetation has undergone major and rapid changes in recent times, and this is a result of repeated Māori burning, farming, pressures from browsing/pest animals (primarily rabbits, goats and rats) and accidental fires in the 1970s (Ogle 1990). Most of the original vegetation has been replaced by secondary forest and fern/grasslands, with a few patchy forest remnants found only on steep coastal cliff sides and gullies. Based on remnant stand composition and vegetation types present in adjacent areas, it is likely that *Metrosideros* forest was previously dominant with a component of *Litsea*, *Vitex* and *Dysoxylum* also in the canopy (Parris & Lynch 1971).

2.4.9 Pataua Island Scientific Reserve

Pataua Island is a small hilly 29.4 ha island, located within the Ohiwa Harbour. The island is adjacent to the mainland, separated only by intertidal mangrove shrub-land and mudflats. Despite the islands small size it hosts an interesting range of coastal vegetation types. Coastal *Metrosideros*–broadleaved forest dominates the steep and exposed western/harbour side (with a small area *Dacrycarpus dacrydioides* dominated forest in a low-lying depression). Large remnant *Metrosideros* fringe the western side of the island and overhang the harbour, with a younger cohort of trees present on the cliffs above. It is likely Māori cleared the forest via burning c. 200 years ago and consequently secondary *Kunzea–Knightia* forest is the dominant vegetation type present on the remainder of the island, particularly on the ridge tops and sheltered eastern side. Areas of shrub/sedgeland dominate the gentle fringing slopes of the southwest side of the island; species here include small leaved *Coprosma* spp. (*C. propinqua*, *C. tenuicaulis*, *C. robusta* x *C. tenuicaulis*), *Olearia solandri*, *Baumea juncea*, and *Typha orientalis* (Clarkson & Regnier 1989; Cashmore 2010).

2.4.10 Oroi Scenic Reserve and Opape Coastal Walkway

The Oroi Scenic Reserve is covers 19.5 ha and consists of a narrow rectangular strip of hilly terrain, continuous with forest on Ngai Tamahaua hapu land along the Opape Coastal Walkway. The forest was completely burnt off c. 200 years ago, and partially burnt again c. 100 years ago. Vegetation consists of mature

second growth semi-coastal *Beilschmiedia–Knightia–Vitex* forest on inland ridges and hillslopes, with mixed age *Metrosideros* forest dominating the steep rocky cliffs and headlands. Areas of *Leptospermum* scrub are also present, particularly in the western quarter of Oroi Scenic Reserve, where disturbance has been the greatest (Clarkson & Regnier 1989; Wildland Consultants 2006).

2.4.11 Great Barrier Island (Aotea)

Although not within the focus study region, *Metrosideros* forest on Great Barrier Island (Hauraki Gulf, New Zealand) was also surveyed, for the purpose of comparison. Great Barrier Island is the fourth largest island in the New Zealand archipelago (c. 28,500 ha), and situated in the outer Hauraki Gulf, some 100 km north east of Auckland. The islands interior is steeply dissected with several volcanic peaks, the highest, Mount Hobson, exceeds 600 m asl (Marjoribanks 1976). With the exception of cleared areas for dwellings and pasture, Great Barrier Island is predominantly covered in native vegetation. The current vegetation pattern is a result of a long history of intense and widespread human modification. The forest has been burnt several times in the past, accordingly much of the island is covered in is *Kunzea* and/or *Leptospermum* regenerating forest, with *Cyathea dealbata* frequently dominating the sub-canopy. Mature broadleaf forest remnants can be found in the steep gullies and at high altitudes where the effect of burning and logging was less severe. *Metrosideros* forest is the dominant canopy tree on the coastal cliffs and headlands; understories are usually sparse, characteristic species include *Macropiper excelsum*, *Pseudopanax crassifolium*, *Pseudopanax lessonii* and *Geniostoma* (Ogden et al. 2010).

Chapter Three: Forest structure and composition

3.1 Introduction

Indigenous forest was thought to cover c. 85%–90% of New Zealand's land surface in the pre-settlement era but currently only c. 23% of New Zealand's land surface retains indigenous forest (McGlone 1989). This decline is primarily a result of 19th century anthropogenic disturbances, such as historic fire, logging and land clearance. However remaining forest is still under threat, and continues to be adversely affected by invasion of adventive species, fire, land use change and loss of ecosystem processes (Walker et al. 2006; Wiser et al. 2011). For this reason, data which quantifies the current composition, structure and extent of the ingenuous forest communities is vital, as this underpins resource description, land-use planning and conservation management (Allen et al. 2003).

A number of studies have contributed to the national reporting of quantitative data describing the structure and composition of New Zealand's forest and scrubland communities (e.g., McKelvey & Nicholls 1957; Nicholls 1976; Wiser & Hurst 2008; Wiser et al. 2011), though very little emphasis is placed on *Metrosideros* forest. For example, a classification of New Zealand forest and shrub-lands, based on a national 8-km grid plot sampling method (Wiser & Hurst 2008) gave no mention of *Metrosideros* forest, whilst other studies (McKelvey & Nicholls 1957; Nicholls 1976) failed to concisely describe the forest type due to its intricate and varied vegetation patterns, choosing instead to group *Metrosideros excelsa* with "general hardwoods". The lack of basic structure and composition data for *Metrosideros* forest is unexpected for a forest type dominated by a species revered in New Zealand culture, and considered to be rare and in a state of decline (Hosking & Simpson 2011).

3.2 Aims and objectives

The objective of this chapter was to address the current lack of structural and compositional data for *Metrosideros* forests and provide a baseline for future research. This was achieved via a large scale survey of island and coastal *Metrosideros* forests in the Bay of Plenty Region, whereby quadrats were located

with a Global Positioning System (GPS) and main stems were mapped to allow for future re-measurement. The specific aims of this chapter are:

(1) Provide new quantitative information on the structure and composition of *Metrosideros* forests in the Bay of Plenty;

(2) Classify *Metrosideros* forest types present in the region and identify relationships, if any, between forest types and site variables;

(3) Compare and contrast *Metrosideros* forest in the Bay of Plenty, with other forests, both regionally and nationally.

3.3 Methodology and Analysis

3.3.1 Forest survey

A comprehensive forest survey using a quadrat based method was conducted in the Bay of Plenty Region, between February and November 2011; with the exception of data collection on Tuhua, which occurred in December 2009. Sites were selected to cover the full extent and age range of coastal and island *Metrosideros* forest in the region; site locations extended from Waihi Beach eastwards to Opape. *Metrosideros* forest on Great Barrier Island (Hauraki Gulf) was also surveyed to provide data on an outlying population, for the purpose of study completeness and comparison. Data collection was unintentionally skewed towards populated areas, where the majority of managed reserves exist. Much of the eastern Bay of Plenty (Opotiki to Lottin Point) was omitted from this study, despite the fact this is where some of the most extensive stands of *Metrosideros* are located. The majority of forested land eastwards of Opotiki is privately owned by multiple land owners and iwi groups, and thus permission to undertake research could not be obtained. It would have been useful to determine forest ages, however as *Metrosideros* wood is too hard for normal increment coring this was not feasible. As an alternative, stem disks were taken from a small number of fallen trees in region.

3.3.2 Quadrat positioning and survey procedure

The distribution of *Metrosideros* within studied forests was easily identified on aerial photographs; often individual trees were able to be recognised due to their large size and pillowy texture of their canopy. *Metrosideros* was more dominant in the coastal fringe/zone of the forests, and became less common inland. Quadrats within accessible coastal zones were objectively located using randomly generated coordinates. *Metrosideros* assemblages also occurred sporadically among coastal/lowland forest; to capture these areas a stratified sampling approach was used, specifically targeting areas dominated by *Metrosideros* and rejecting sites where it was uncommon.

For a site to be considered suitable for this study, *Metrosideros* was required to contribute ≥50% to canopy foliage area. Due to the large and sprawling nature of *Metrosideros* canopies, a single tree within the quadrat could fulfil this criterion.

Quadrat slopes ranged from 0–45°; *Metrosideros* commonly occupied slopes much steeper than this, including near vertical faces. However slopes greater than 45° were found unsuitable for the quadrat based sampling method used in this study. Quadrats were orientated and aligned with topographic contours where possible, and care was taken not to cross major topographic/geomorphic boundaries. The total number of quadrats measured within each reserve/forest was dependant on stand size and variability.

Forest quadrats were predominantly 400 m^2 (20 × 20 m), the commonly accepted standard for lowland forests in New Zealand (Hurst & Allen 2007). This was amended in the field when topographic barriers and steepness constrained the area which could be sampled, thus retaining site homogeneity. In all quadrats, site characteristics such as slope, aspect, physiography and drainage were recorded. Within each quadrant all species with stems ≥2.0 cm diameter at breast height (breast height = 130 cm) were measured using a soft calibrated tape measure. In a 100 m^2 (10 × 10 m) randomly chosen subsection of the quadrat, stems ≥30 cm in height but <2.0 cm dbh (hereafter referred to as saplings) were tallied, tree and shrub species <30 cm tall were also tallied (hereafter referred to as seedlings). Seedlings without fully developed leaves were excluded from counts. Epiphytic and climbing species were ranked according to their percentage relative dominance. Similarly, ground covering species (e.g. grasses, ferns and seedlings) were also ranked based on their percentage relative dominance on the ground. The percentage contribution of litter, bare ground, exposed rock, non-vascular and vascular vegetation on the ground was also noted. Canopy height, emergent height and percentage canopy cover was estimated for each quadrat and additional notes such as the presence of herbivore browse/ stock damage noted. GPS coordinates were taken in the upper left hand corner of each quadrat and a sketch map completed showing the position of the main trees.

Sites of *Metrosideros* regeneration were uncommon, substantial numbers of seedlings were only observed on coastal cliffs on Moutohora and on stream terraces in the Matata Scenic Reserve. Thus three additional quadrats of variable size (ranging from 50–100 m^2) were randomly located along Awataraiki Stream terrace (Matata Scenic Reserve) with the purpose of capturing compositional trends of early *Metrosideros* colonisation.

3.3.3 Forest classification

For each quadrat, basal area and density were calculated for *Metrosideros* and associated species with stems >2 cm dbh. Multivariate ordination was then used to detect complex relationships between vegetation and site variables (Appendix 1 and 2); survey data was analysed using NMS (Non-metric Multidimensional Scaling) ordination software (PC-ORD ver. 6 software). NMS is a method of indirect gradient analysis in which study sites are mapped in reduced ordination space according to the rank order of compositional distances between them. This type of analysis has an advantage over other ordination techniques (e.g. Principal Component Analysis) in examining ecological data because it maximises a rank order correlation as opposed to maximising linear correlations, does not ignore community structure that is unrelated to environmental variables and is robust with respect to zero rich data sets (Robbins and Mathews 2010; Youngblood et al. 2006). Analysis was carried out on stem density data (stems >2 cm dbh) as opposed to basal area data because *Metrosideros* undergoes a process of natural self-thinning (Clarkson & Clarkson 1994), thus a young stand comprising many small *Metrosideros* trees may have a similar basal area to a mature forest with a single large *Metrosideros* specimen, and structural differences would be masked.

Dead stem densities were included in the analysis; however these remained distinct from species live stem densities. Rarely occurring species, i.e., those that occurred in less than 5% of quadrats, were removed to reduce noise in the data set. The reduced data set was then generally relativized to make the total species density in each plot equal to one (P=1). Sorensen distance was chosen as the measure of compositional dissimilarity between quadrats and a Monte Carlo test of 400 randomisations was used to determine how likely the observed stress value of the final solution would occur by chance alone.

The joint-plot function (McCune and Mefford 2011) was used to overlay environmental vectors associated with the vegetation composition. Vector direction indicates directionality of influence and vector length is representative of the variable's explanatory power. To improve the clarity of the graphical display, the ordination diagrams were rotated to place the variables of interest parallel with the ordination axis. Site variables included: canopy condition, which was established from EBOP (2009) photo-monitoring scores and observation in the

field; percentage rock, estimated in field; stand age, approximated using diameter growth relationships (Chapter Four); stand and *Metrosideros* density/basal area, calculated from vegetation survey data. These variables were only displayed on the ordination diagram when they were deemed significant (r^2 >0.30).

To aid interpretation of the NMS ordination, and to determine whether species composition was organised into discrete vegetation types, a cluster analysis was also performed on the same relativized data matrix. Cluster analysis allowed quadrants to be grouped based on the similarity between the redundant patterns of their responses. Cluster analysis was also performed in PC-ORD ver. 6 software (McCune and Mefford 2011), and as in the NMS analysis, plots were clustered on Sorensen dissimilarities, making the result directly comparable. The Atkinson (1985) vegetation classification system was used to name the vegetation type associated with each of the ten groups. A description of the vegetation within each group is also provided.

3.4 Results

3.4.1 Field survey and observations

A total of 35 quadrats were measured during this study, resulting in a total survey area of 14,200 m^2. Quadrats ranged in area from 50–400 m^2, with the majority (>80%) being 400 m^2 (20 × 20 m). Quadrat slopes ranged from 0–50° and quadrat altitudes ranged from 18–150 m asl. Specific site variables and locations are given in Appendix 1 and 2. *Metrosideros* scrub commonly dominated extremely steep, rocky and drought prone sites, where few other species were present. The precarious nature of such sites meant a quadrat based method was unsuitable. Sampling was instead focussed on *Metrosideros* forest, which hosted a more diverse range of associated species. *Metrosideros* forest was the dominant vegetation type on the coastal headlands, cliffs and islands in the Bay of Plenty coastal zone. The occurrence of *Metrosideros* forest generally decreased inland, where species such as *Knightia*, *Beilschmiedia* and *Dysoxylum* subsequently replaced *Metrosideros* in the canopy. Localised patches of *Metrosideros* forest occurred intermittently within this vegetation, where trees had colonised following a slip or landslide; slip scars were always evident and slopes generally exceeded 30°.

3.4.2 Flora

The total number of vascular species recorded in this survey was 133. Of these, 122 were indigenous, and the remaining 11 were adventive; adventive species were restricted to recently disturbed sites, or near forest margins. Generally all species were common lowland or coastal species. However, two species listed as threatened were recorded (de Lange et al. 2009). These were *Pimelea tomentosa* and *Olearia pachyphylla*; both were found in Opape quadrats. The small tree species *Pittosporum umbellatum* also had a localised distribution, and was only found within Orokawa Scenic Reserve quadrats, where it was a common sub-canopy species.

Of the 133 species identified, 34 were ferns, seven of which were found growing both epiphytically and terrestrially. A total of 20 epiphyte species were identified; these were more common in mature *Metrosideros* forest and away from the coast. All but three of the tree species were angiosperms and of the conifer species detected, only *Dacrycarpus dacrydioides* had stems >2 cm dbh.

Although the total number of indigenous species identified was high, the majority represented only a minor component of the vegetation. Common and widespread species within *Metrosideros* forest included: *Coprosma macrocarpa*, *Coprosma robusta*, *Cyathea dealbata*, *Beilschmiedia*, *Dysoxylum*, *Melicytus ramiflorus*, *Myrsine*, *Litsea*, *Pseudopanax lessonii*, *Pseudopanax arboreus* and *Knightia.* These species were significant components of understory and sub-canopy of sampled stands, with *Beilschmiedia*, *Dysoxylum* and *Litsea* also contributing to the canopy in some locations, such as in Ohope Scenic Reserve, Kohi Point Scenic Reserve and Pikowai.

Table 3.1: Full species list for all sites, compiled from survey data

Species identified in survey quadrats		
Native tree/shrub species	*Phyllocladus trichomanoides*	*Pterostylis banksii*
Alectryon excelsus	*Pimelea tomentosa*	*Pyrrosia eleagnifolia*
Aristotelia serrata	*Pittosporum crassifolium*	*Tmesipteris elongata*
Beilschmiedia tarairi	*Pittosporum tenuifolium*	**Monocots**
Beilschmiedia tawa	*Pittosporum umbellatum*	*Astelia banksii*
Brachyglottis repanda	*Prumnopitys ferruginea*	*Astelia solandri*
Carmichaelia australis	*Pseudopanax* hybrid	*Baumea tenax*
Carpodetus serratus	*Pseudopanax arboreus*	*Carex diandra*
Coprosma arborea	*Pseudopanax crassifolius*	*Carex testacea*
Coprosma grandifolia	*Pseudopanax lessonii*	*Collospermum hastatum*
Coprosma lucida	*Rhopalostylis sapida*	*Dianella nigra*
Coprosma macrocarpa	*Schefflera digitata*	*Drymoanthus adversus*
Coprosma repens	*Sophora microphylla*	*Earina mucronata*
Coprosma rhamnoides	*Vitex lucens*	*Gahnia setifolia*
Coprosma robusta	*Weinmannia racemosa*	*Ichthyostomum pygmaeum*
Coprosma spathulata	**Ferns and fern allies**	*Juncus* spp.
Coriaria arborea var. *arborea*	*Adiantium cunninghamii*	*Libertia ixioides*
Corynocarpus laevigatus	*Adiantum hispidulum*	*Machaerina sinclairii*
Dacrycarpus dacrydioides	*Asplenium bulbiferum*	*Oplismenus hirtellus var. imbecillus*
Dodonaea viscosa	*Asplenium flaccidum*	*Phormium cookianum* subsp. *hookeri*
Dysoxylum spectabile	*Asplenium haurakiense*	*Phormium tenax*
Entelea arborescens	*Asplenium oblongifolium*	*Poa anceps*
Freycinetia banksii	*Asplenium polyodon*	*Uncinia uncinata*
Geniostoma rupestre	*Blechnum chambersii*	*Cordyline australis*
Hebe stricta var. stricta	*Blechnum filiforme*	**Lianes and climbers**
Hedycarya aborea	*Blechnum fluviatile*	*Clematis foetida*
Helichrysum lanceolatum	*Blechnum novae-zelandiae*	*Clematis paniculata*
Knightia excelsa	*Cyathea dealbata*	*Metrosideros perforata*
Kunzea ericoides	*Cyathea medullaris*	*Muehlenbeckia australis*
Leptecophylla juniperina	*Dicksonia squarrosa*	*Muehlenbeckia complexia*
Leptospermum scoparium	*Diplazium australe*	*Parsonsia heterophylla*
Leucopogon fasciculatus	*Doodia australis*	*Ripogonum scandens*
Litsea calicaris	*Gleichenia microphylla*	**Herbs**
Macropiper excelsum	*Hymenophyllum demissum*	*Drosera auriculata*
Melicope ternata	*Hymenophyllum revolutum*	**Adventives**
Melicytus micranthus	*Lycopodium deuterodensum*	*Ligustrum sinense*
Melicytus novae-zelandiae	*Microsorum pustulatum*	*Racosperma mearnsii*
Melicytus ramiflorus	*Microsorum scandens*	*Ulex europaeus*
Metrosideros excelsa	*Paesia scaberula*	*Asparagus* spp.
Metrosideros robusta	*Pneumatopteris pennigera*	*Hedychium flavescens*
Myoporum laetum	*Polystichum richardii*	*Lonicera japonica*
Myrsine autralis	*polystichum* spp.	*Prunnis* spp.
Nothofagus truncata	*Psilotum nudum*	*Ehrharta erecta*
Olearia albida	*Pteridium esculentum*	*Cortaderia jubata*
Olearia pachyphylla	*Pteris macilenta*	*Cortaderia selloana*
Olearia rani var. *colorata*	*Pteris tremula*	

3.4.3 Quadrat ordination and classification

Cluster analysis

To define coherent vegetation groups within the quadrat data, the dendrogram (Figure 3.1) was pruned at a level where c. 35% of the matrix information remained. At this level, 10 distinct vegetation groups were delineated, representing a compromise between homogeneity of the groups and the number of groups defined (McCune & Grace 2002). The Atkinson (1985) vegetation classification system was applied to the ten vegetation groups (Table 3.2). The derived groups were ecologically interpretable in that they contained quadrats from geographically close locations, often within the same reserve, or they contained quadrats in similar aged stands. The majority of Tuhua quadrats and all Moutohora quadrats formed distinct groups and the bulk of the Ohope Scenic Reserve quadrats and the nearby Kohi Point Reserve quadrats were grouped within three adjacent clusters, separated by c. 5% of information.

Table 3.2: Vegetation groups identified by cluster analysis and the Atkinson (1985) vegetation classification system.

Legend ref. (group)	Forest type	No. quadrat
1	*Metrosideros/ Pseudopanax lessonii* forest	4
2	*Metrosideros/ Melicytus ramiflorus – Pseudopanax lessonii* forest	4
3	*Metrosideros/ Myrsine australis – Myrsine ramiflorus* forest	5
4	*Metrosideros/ Myrsine australis – Coprosma macrocarpa – Coprosma lucida* forest	5
5	*Metrosideros/ Melicytus ramiflorus – Cordyline australis* forest	3
6	(*Kunzea*) *Metrosideros/ Pseudopanax arboreus – Pseudopanax lessonii* forest	4
7	(*Knightia*) *Metrosideros/ Myrsine australis– Melicytus ramiflorus* forest	6
8	*Metrosideros/ Coprosma macrocarpa – Cyathea dealbata – Myrsine australis* forest	7
9	*Metrosideros/ Dysoxylum spectabile– Beilschmiedia tawa– Cyathea dealbata* forest	3
10	(*Cortaderia jubata*) *Coriaria arborea/ Metrosideros – Coprosma robusta* scrub	2

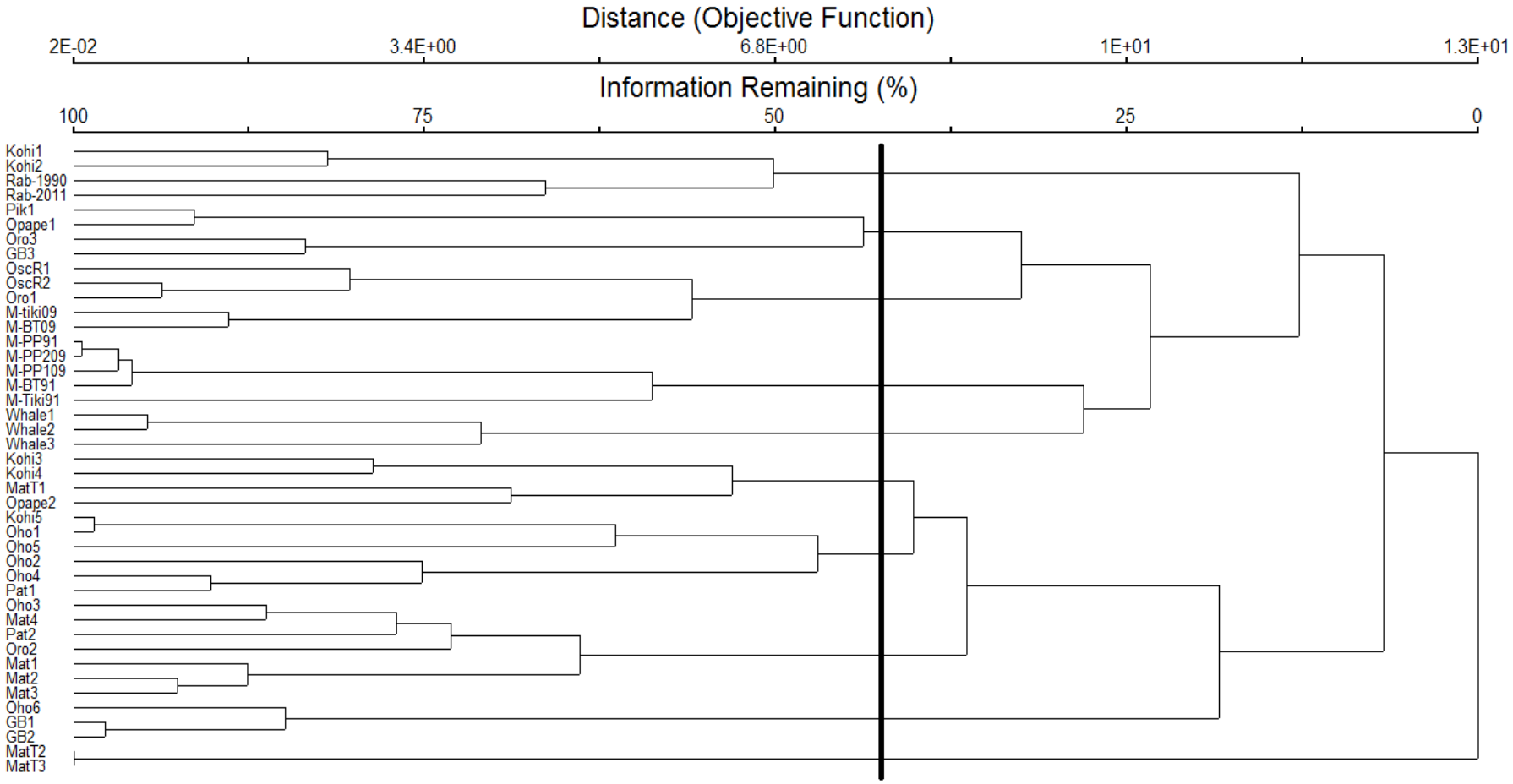


Figure 3.1: Dendrogram resulting from a cluster analysis of 32 species in 39 quadrats (including re-measurement data from four permanent quadrats), located in the Bay of Plenty and Great Barrier Island, using relative Sorensen distance and the Flexible Beta Linkage group method. Black line indicates the distance that dendrogram was pruned and the ten forest groups were defined.

3.4.4 Forest types

Group 1

Coastal *Metrosideros/Pseudopanax lessonii* forest

This forest type was found in Kohi Point and Motuotau reserves, and all quadrats were within 100 m from the sea. The vegetation had a very simple structure and comparably low species richness. *Metrosideros* had a density range of 150–775 stems ha^{-1} and formed a tight canopy 15–18 m high. Typically *P. lessonii* formed an understory and sub canopy up to 10 m, with only minor contributions from other taxa, including *Coprosma* spp. and *Pseudopanax crassifolium*. Ground cover species were sparse but commonly included *Adiantium cunninghamii*, *Asplenium oblongifolium*, and *Microsorum pustulatum*.

Figure 3.2: *Metrosideros excelsa* forest located at (left) Kohi Point Reserve and (right) Motuotau. The dominance of *Pseudopanax lessonii* in the forest understory makes forest at these two locations appear very similar.

Group 2

Coastal *Metrosideros/Melicytus ramiflorus–Pseudopanax lessonii* forest

This forest type included quadrats from Great Barrier Island, Orokawa Scenic Reserve, Pikowai and Opape. All quadrats, except that at Pikowai, were within 50 m of the sea. The number of species within each quadrat was varied, however was generally much higher than that of the other vegetation groups identified, in part this was due to a high number of ferns an epiphytes. *Metrosideros* densities ranged from 900–1150 stems ha^{-1} with the exception of the Pikowai site where it did not exceed 25 stems ha^{-1}; the vegetation here was deemed to be more mature. Canopies ranged from 12–18 m. *Melicytus ramiflorus* and *P. lessonii* were common in the understory and reached c. 8 m in height. Other common understory species included *Kunzea*, *Leucopogon fasciculatus* and *Myrsine*

australis. The Pikowai site also had a very strong presence of *Litsea* seedlings and saplings. Ground cover species included *Adiantium cunninghamii*, *Asplenium polyodon*, *Machaerina sinclairii* and *Microsorum scandens*,

Figure 3.3: *Metrosideros excelsa* forest located at (left) Orokawa Scenic Reserve and (right) Ngai Tamahaua Hapu land, Opape.

Group 3

Semi–coastal *Metrosideros*/*Myrsine australis*–*Melicytus ramiflorus* forest

This forest type was present on Tuhua, the adjacent Orokawa Scenic Reserve on the mainland and also in Oscar Reeves Scenic Reserve, Ohiwa. The density of *Metrosideros* stems ranged from 25–666 stems ha^{-1}, and formed dense canopies not exceeding 20 m. Few *Weinmannia racemosa* individuals were present, contributing to the canopy, as were emergent *Knightia*. Typically *M. australis*, *M. ramiflorus* and *P. lessonii* formed the majority of the understory. However, other species such as *Coprossma macrophylla*, *Litsea* and *Hedycarya* were also common. Ground cover vegetation varied between quadrats, but generally included *Machaerina sinclairii* on banks, and *Doodia australis* and *Adiantium cunninghamii* on the forest floor.

Figure 3.4: *Metrosideros excelsa* forest located on (left) Tuhua, and (right) Orokawa Scenic Reserev, Waihi Beach Both forests have a strong presence of *Myrsine australis* and *Melicytus ramiflorus* in the understory.

Group 4

Semi–coastal (*Knightia*) *Metrosideros*/*Myrsine–Coprossma macrocarpa* forest

This forest type was comprised solely of Tuhua quadrats and is similar in composition to vegetation Group 3. *Metrosideros* formed a canopy 14–20 m often with emergent *Knightia*. The density of *Metrosideros* ranged from 375–825 stems ha^{-1}, and stem diameters ranged from 15–112 cm dbh. *Myrsine australis, C. macrocarpa* and *Coprosma lucida* dominated the understory vegetation. Other common understory species included *Geniostoma, M. excelsum, Pseudopanax arboreus* and *Melicytus ramiflorus*. *Litsea* was also often present in low numbers in the shrub layer, however was prolific as seedlings. Common ground cover species included *A. polyodon, Doodia australis* and *Astelia banksii*.

Figure 3.5: *Metrosideros excelsa* forest located on Mayor Island.

Group 5

Coastal *Metrosideros*/*Melicytus ramiflorus–Cordyline australis* forest

This forest type was restricted to Whale Island quadrats, where the majority of forest is known to be less than 40 years old. The vegetation had a simple structure and had low species richness compared to other vegetation types. The density of *Metrosideros* stems ranged from 1100–2825 stems ha^{-1}, with an additional 175–1175 dead standing stems also present; this was the highest *Metrosideros* density of all vegetation groups. *M. ramiflorus* and *C. australis* formed the understory and sub canopy, with some individuals also contributing to the canopy of c. 12 m. Additional understory species included *M. ramiflorus, P. lessonii* and *Geniostoma*. Ground cover species were sparse, with *Microsorum pustulatum* being the most common, followed by *A. oblongifolium.*

Figure 3.6: Young, high density *Metrosideros excelsa* forest located near McEwens Bay, Whale Island.

Group 6

Coastal (*Kunzea*) *Metrosideros*/*Pseudopanax arborea*–*Pseudopanax lessonii* forest

This forest type contained quadrats located in the Matata Scenic Reserve, Kohi Point Reserve and also Opape. The density of *Metrosideros* ranged from 400–1250 stems ha^{-1}; however total stem density was the highest of all groups. Few emergent *Knightia* were also present and scattered *Kunzea* commonly contributed to the canopy. The understory was very dense and predominantly comprised of small trees and shrubs of *P. arboreus* and *P. lessonii* and *Cyathea dealbata*. Other understory species included *C. lucida, Geniostoma* and *Brachyglottis repanda.* The ground cover was predominantly composed of *Geniostoma* and *C. lucida* seedlings; however *Machaerina sinclairii* was also common on cliffs and banks within the quadrats and *Adiantium cunninghamii* was common on the forest floor.

Figure 3.7: *Metrosideros excelsa* forest located at (left) Matata Scenic Reserve and (right) Ngai Tamahaua Hapu land, Opape. Both forests had *Pseudopanax arborea* and *Pseudopanax lessonii* dominated understories. *Kunzea* was also common in the understory and canopy of the Matata site.

Group 7

Semi–coastal (*Knightia*) *Metrosideros*/*Myrsine*–*Melicytus ramiflorus* forest

This forest type predominantly contained quadrats located in the Ohope Scenic Reserve, however also included quadrats from the neighbouring Kohi Point Reserve and Pataua Island Scientific Reserve. *Metrosideros* densities range from 150–325 stems $ha^{-1}$and form dense canopies up to 20 m; often with emergent *Knightia*. *Myrsine australis* and *M. ramiflorus* are the most common understory species; however *P. lessonii*, *B. repanda* and *Geniostoma* were also common. *Litsea* juveniles were present in all quadrats, with some reaching 10 cm dbh. *Litsea* was often one of the most prolific seedling and sapling species.

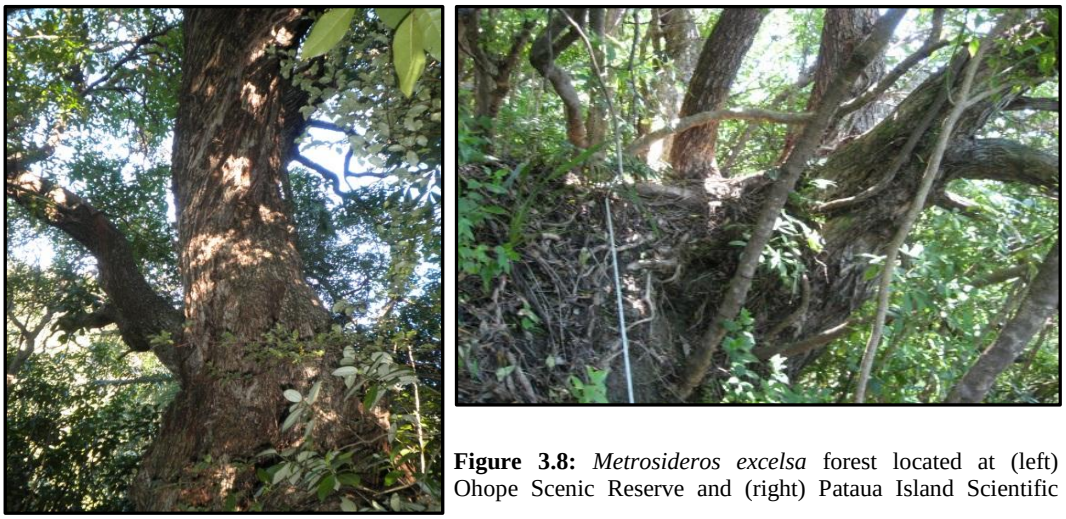


Figure 3.8: *Metrosideros excelsa* forest located at (left) Ohope Scenic Reserve and (right) Pataua Island Scientific

Group 8

Semi–coastal *Metrosideros*/*Coprosma macrocarpa*–*Cyathea dealbata*–*Myrsine* forest

This forest type predominantly contained quadrats from Matata Scenic Reserve and all were on hill-slopes >30°. *Metrosideros* trees were present at comparatively low densities, ranging from 50–200 stems ha^{-1}. Few *Weinmannia racemosa* individuals were present, particularly in quadrats located on slip scars; stem appeared a similar age to those of *Metrosideros* and are likely to have been inited by the same disturbance event. Understory species varied between quadrats; however dominance of *C. macrocarpa, C. dealbata and M. australis* was a commonality. Ferns such as *A. cunninghamii* and *B. novae-zelandiae* were also common in the ground tier, as were juveniles of *B. repanda, M. excelsum* and *M. ramiflorus*. Seedlings of *Beilschmiedia*, *Litsea* and *Dysoxylum* were also present

in low numbers. Unlike many of the other vegetation groups epiphytes species were common, although in low numbers.

Figure 3.9: *Metrosideros excelsa* forest located at Matata Scenic Reserve. Forest comprised a sparse ground and shrub layer, overtopped by a sub-canopy of tree ferns, predominantly *Cyathea dealbata.*

Group 9

Semi–coastal *Metrosideros*/*Dysoxylum*–*Beilschmiedia*–*Cyathea dealbata* forest

This forest type contained quadrats located Ohope Scenic Reserve and on Great Barrier Island, all were within mature forest, >400 m from the coast. *Metrosideros* is present as large trees at very low densities, not exceeding 25 trees ha^{-1}, consequently the large stem size contributed to this vegetation group having the average highest basal area (111.5 m^2 ha^{-1}). The canopy is predominantly *Metrosideros* with small contributions from much younger *Dysoxylum* and *Beilschmiedia*. In the Great Barrier Island quadrats *Beilschmiedia tarairi* was also present. These species also contribute to the understory as well as other commonly occurring species such as *Rhopalostylis sapida*, *Corynocarpus* and *C. dealbata*. This vegetation type also has a comparably large number of ground covering ferns and epiphyte species such as *Adiantium cunninghamii*, *Asplenium polyodon*, *Microsorum pustulatum*, and *Microsorum scandens*.

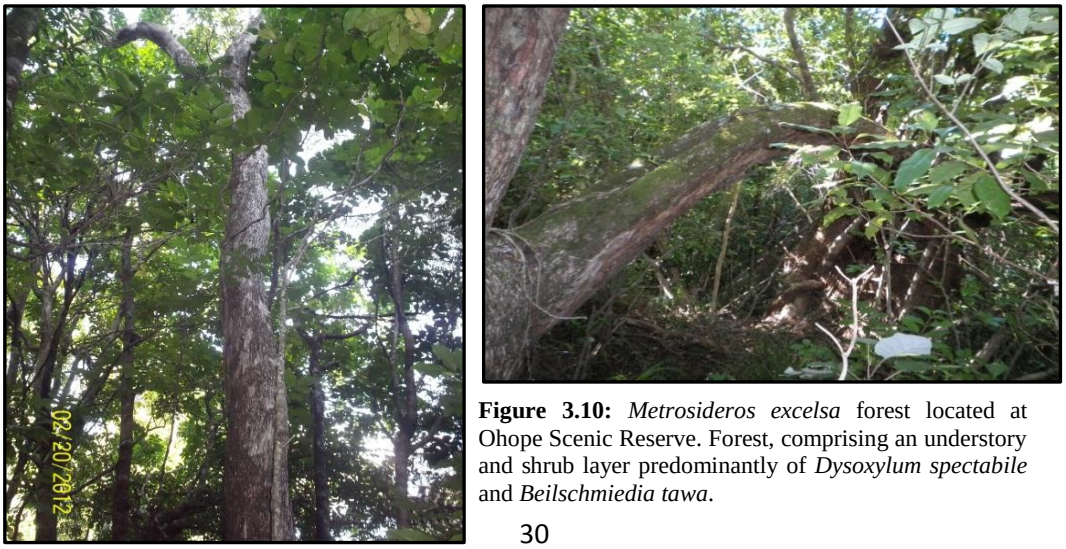


Figure 3.10: *Metrosideros excelsa* forest located at Ohope Scenic Reserve. Forest, comprising an understory and shrub layer predominantly of *Dysoxylum spectabile* and *Beilschmiedia tawa*.

(*Cortaderia jubata*) *Coriaria arborea/ Metrosideros–Coprosma robusta* scrub

This forest type was present along the stream margins in the Matata Scenic Reserve, particularly the Awataraiki stream where previously severe debris flows stripped the stream terraces back to bedrock. *Metrosideros* forest dominated the adjacent gully edges and hill-slopes. *Coriaria arborea* and scattered *C. jubata* formed a discontinuous canopy up to 3 m. beneath this, and in the intermittent light gaps *Metrosideros* seedlings and saplings were present, with densities up to 1620 individuals' ha^{-1}. *Coprossma robusta* individuals were also found throughout, as were *Hebe stricta*, *Knightia* and *Weinmannia racemosa*, however at lower densities.

Figure 3.11: *Metrosideros excelsa* regeneration sites, located along the Awataraiki stream channel, Matata Scenic Reserve.

Table 3.3: Forest and site variables for vegetation groups identified by cluster analysis. Density and basal area measures are for stems > 2 cm dbh. Species richness is equal to the total number of species per 400 m^2.

Forest group	Group total (± SD)			Group Range			
	Density (stems ha^{-1})	Basal Area (m^2 ha^{-1})	Species richness	Elevation (m)	Slope (°)	Age (years)	Canopy height (m)
1	5271 ± 1260	54.5 ± 19.9	14 ± 2	35–55	20–60	55–180	15–18
2	3793 ± 580	56.3 ± 27.2	27 ± 5	18–60	5–30	35–300+	14–18
3	4841 ± 1821	88.0 ± 49.5	26 ± 9	40–75	2–25	105–300+	14–20
4	5160 ± 1650	82.1 ± 18.7	17 ± 3	40–60	2–10	60–225	14–20
5	4475 ± 884	46.8 ± 3.9	15 ± 3	20–55	2–7	30–40	11–13
6	5318 ± 1050	49.5 ± 30.6	20 ± 3	15–75	10–40	20–190	12–20
7	4630 ± 1752	79 ± 26.7	27 ± 2	20–70	0–40	60–200	17–20
8	3277 ± 1226	74.8 ± 25.9	25 ± 5	20–70	30–40	35–300+	15–20
9	1891 ± 656	111.5 ± 60.8	25 ± 6	30–60	10–15	300+	18–22
10	3100 ± 424	6.1 ± 1.4	16 ± 1	12–20	0–5	< 10	2–3

3.4.5 Ordination of quadrats

Non-metric Multidimensional Scaling (NMS) was used to ordinate quadrats based on species stem density. A Monte Carlo test of 500 runs with randomized data indicated the minimum stress of a 3-D solution was lower than would be expected by chance (P = 0.0040). Thus a satisfactory three-dimensional NMS ordination solution was obtained; this had a final stress and instability value of 16.37 and 0.000001, respectively. The final three-dimensional solution is shown in Figure 3.2. The coefficients of determination for the correlations between ordination matrix distances and distances in the original data matrix are shown in Table 3.4. The three axes cumulatively explain 58% of the total variance in the data set. The largest proportion of variation is explained by axis 1, which shows a positive association with the percentage of bare exposed rock in the quadrats; however this axis is incoherent with the vegetation groups identified in the cluster analysis. Of all the species included in the analysis, *C. robusta* had the strongest association with this axis (r = 0.784) followed by *Litsea* which showed a weak negative relationship (r = -0.341); no other species showed a robust correlation with axis 1 (Table 3.5). The strong positive association between *C. robusta* and bare rock is a likely result of the species preference for forest margins and scrublands; *C. robusta* was found growing in abundance along the Matata stream margins, where rock and thin recent soils were the dominant substrate.

Table 3.4: Coefficients of determination for the three ordination axis.

	r^2	
axis	**Increment**	**Cumulative**
1	0.239	0.239
2	0.133	0.373
3	0.205	0.578

Stand age and *Metrosideros* density were inversely related and were associated with axis 2; this indicates a natural process of self-thinning. Examination of vegetation group change across axis 2 is indicative of the vegetation development and succession through time. Quadrat distance from the sea had a weak correlation with axis 1 (r = <0.30), thus this axis also represents a crude transition

from coastal to semi-coastal/lowland forest also. Broadly this shows a shift from vegetation groups with a strong contribution of *Cordyline australis* (henceforth referred to as *Cordyline*), *P. lessonii* and *M. ramiflorus*, to those with *Myrsine*, *C. macrocarpa* and emergent *Knightia*, with the most mature groups of quadrats comprising an understory and partial canopy of *Dysoxylum, Beilschmiedia* and tree ferns. Examination of individual species correlations with axis 2 revealed *Metrosideros* had a moderate to strong negative relationship (r = -0.571) and *M. australis* a weak negative relationship (r = -0.303) thus these species densities decrease as the forest develops. Conversely *C. dealbata* and *Beilschmiedia* had moderate to strong positive relationships (r = 0.570 and 0.515 respectively) and *Dysoxylum* and *C. medullari*s had moderate positive relationships (r = 0.495 and 0.414 respectively), accordingly the density of these species increases as the forest develops. Species that had weak correlations with axis 1 did not show an increase or decrease in density throughout forest development and thus their occurrences must be attributed to other factors and environmental gradients. The variable "canopy condition" was also shown to be correlated with the quadrat data (Figure 3.2). It is likely this variable is acting as a proxy for pest/possum levels in the stands, as *Metrosideros* canopies are highly susceptible to possum browse. Vegetation change along this vector shows a transition from *Melicytus ramiflorus Pseudopanax* spp. and *Myrsine* in the understory, to *Beilschmiedia*, *Litsea*, *Corynocarpus* and *Dysoxylum* in the understory and as juveniles. This may suggest possum browse on flowers, fruits, seeds and seedlings maybe having an effect on forest regeneration.

Table 3.5: Correlations between Non-metric Multidimensional Scaling ordination axis and species which were present in >5% of survey quadrats. Significant correlations (r > 0.5) are in Bold Type. *d* = dead stems.

Species	Correlation Coefficient (r value)		
	Axis 1	**Axis 2**	**Axis 3**
Beilschmiedia tawa	0.052	**0.515**	-0.121
Brachyglottis repanda	0.057	0.091	-0.120
Coprosma Lucida	-0.280	0.005	-0.280
Coprosma grandifolia	-0.161	0.215	**0.500**
Coprosma macrocarpa	-0.373	-0.141	0.365
Coprosma robusta	**0.784**	-0.010	-0.340
Cordyline australis	0.300	-0.201	0.340
Corynocarpus laevigatus	0.019	0.170	0.171
Cyathea dealbata	0.145	**0.570**	-0.175
Cyathea medullaris	0.170	0.414	0.233
Dysoxylum spectabile	-0.215	0.495	-0.032
Geniostoma rupestre	-0.167	0.020	-0.085
Knightia excelsa	-0.223	0.113	-0.151
Kunzea ericoides	0.317	0.101	-0.246
Leptospermum scoparium	0.252	-0.088	-0.168
Litsea calicaris	-0.341	0.189	0.261
Leucopogon fasciculatus	-0.219	0.098	-0.335
Hedycarya aborea	-0.198	0.313	0.087
Macropiper excelsum	-0.277	0.281	0.439
M. ramiflorus	-0.106	0.241	0.473
Metrosideros excelsa	0.102	**-0.571**	0.369
Metrosideros excelsa (*d*)	0.204	-0.393	0.461
Myrsine australis	-0.023	-2.260	0.334
Olearia rani	0.270	0.171	-0.243
Pittosporum crassifolium	0.056	-0.255	-0.342
Pittosporum tenuifolium	0.291	0.036	-0.209
Pseudopanax arboreus	0.168	-0.072	-0.324
Pseudopanax lessonii	0.205	-0.370	-0.403
Ulex europaeus	0.135	-0.079	-0.146
Weinmannia racemosa	0.062	0.155	-0.176
Vitex lucens	-0.025	0.039	0.412

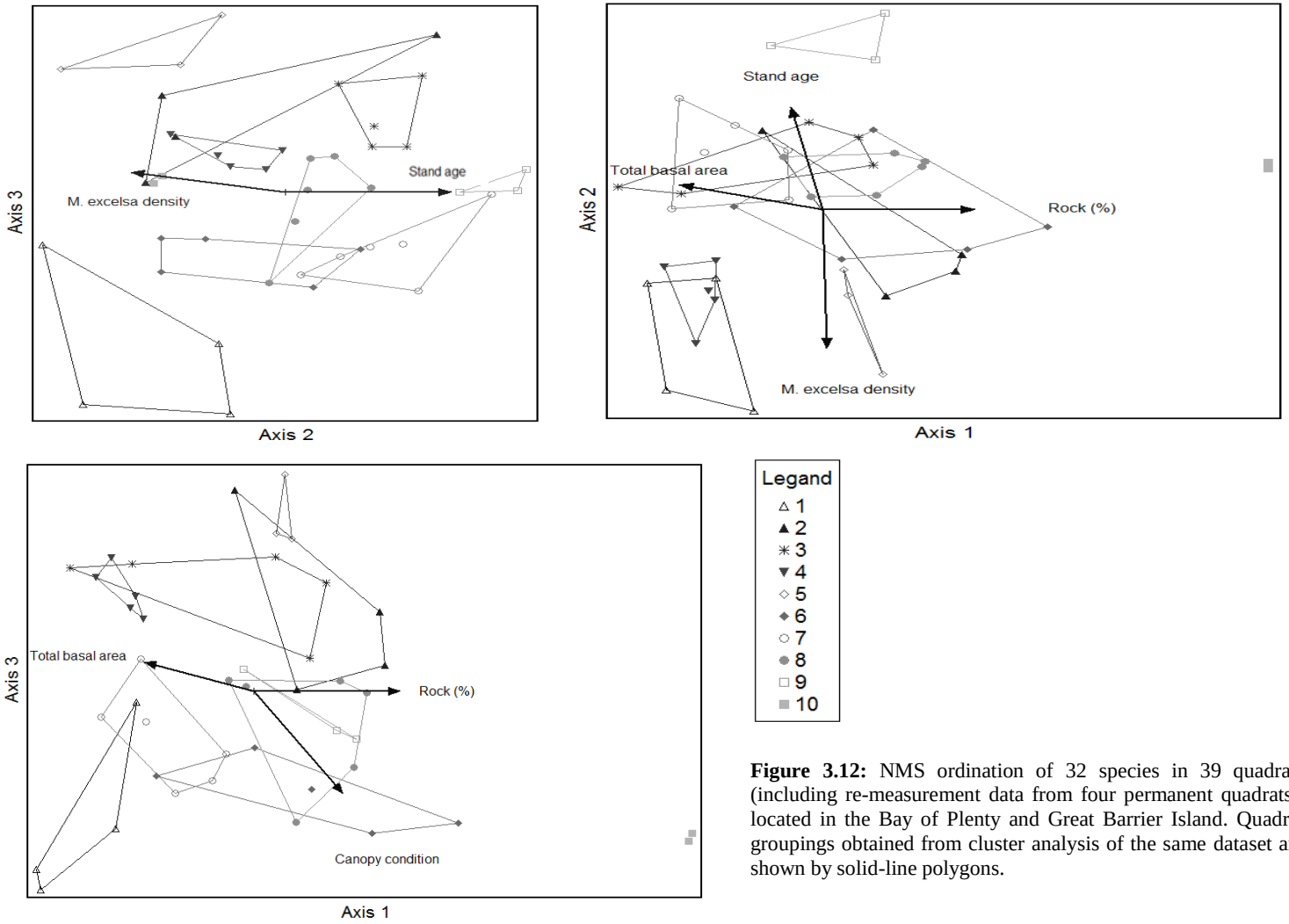


Figure 3.12: NMS ordination of 32 species in 39 quadrats (including re-measurement data from four permanent quadrats), located in the Bay of Plenty and Great Barrier Island. Quadrat groupings obtained from cluster analysis of the same dataset are shown by solid-line polygons.

3.5 Discussion

Comparison of *Metrosideros excelsa* forest in the Bay of Plenty, with other more widespread forest types in New Zealand, highlights the forests unique and varied mix of flora, which in general has low species richness. With the exception of *Kunzea* and *Leptospermum* forests, *Metrosideros* is one of the only forest types in the Bay of Plenty where nearly 100% of canopy cover is contributed by a single species. Many *Metrosideros* stands, particularly those on exposed seaward facing sites had a depauperate flora, with <15 vascular species identified. In part, the low species richness observed in *Metrosideros* forest reflects the harsh and inhospitable sites of which the forest inhabits, as well as the tendency of the *Metrosideros* to retard the rate of which a diverse community can develop (Atkinson 2004). However, compared to *Kunzea* dominated stands on sandy heaths in the region (Smale 1994) *Metrosideros* forest surveyed had a high total number of indigenous species (122 cf. 23). However, understory species richness and composition of Northland *Kunzea* forests, reported by Smale et al. (1995), were more comparable to *Metrosideros* forest in the Bay of Plenty, with c. 9–18 species identified in each 20 x 20 m quadrat, and also a strong presence of *Myrsine australis*, *Pseudopanax lessonii*, *Coprosma macrocarpa* and *Coprosma lucida* in the understory.

Cluster analysis identified 10 distinct groups of quadrats, each containing distinctly different understory vegetation types. The differences in forest structure and composition between groups could be partially explained by geographic position, distance from the sea, topographic landform, as well as site age. This chapter focusses specifically on current *Metrosideros* forest structure and composition and age related variations are discussed in Chapter Five.

3.5.1 Structure and profile

Metrosideros forest structure was simple, and generally comprised a dense sprawling canopy (rarely exceeding c. 20 m in height) with a limited number of species other than *Metrosideros* contributing to canopy foliage. Canopy height was markedly lower in coastal forest compared to semi-coastal forest; this was particularly evident on coastal headlands where the canopy was severely wind shorn and never exceeded 15 m. Emergent *Knightia* individuals were able to

penetrate the tight canopy in some stands, where they reached c. 25 m in height. The presence of *Knightia* was associated with ridgeline topography, such as in Ohope Scenic Reserve, where *Knightia* was a dominant component of the ridgeline vegetation, particularly inland. Likewise on Rangitoto Island, where *Metrosideros excelsa* is the primary rock coloniser, *Knightia* is one of the few species capable of breaching the tight *Metrosideros* canopy, which is indicative of early forest development (Clarkson 1990).

Structure and composition of *Metrosideros* forest understories varied markedly between sites; coastal forest often had a sparse shrub and ground layer, though this became more diverse inland and in more sheltered localities. In general, forest understories comprised of a sparse shrub layer, overtopped by a sub-canopy of either tree ferns in steep inland localities, *Pseudopanax lessonii*, *Coprosma macrocarpa* and *Coprosma lucida* on coastal headlands, or species such as *Myrsine, Beilschmiedia, Dysoxylum* and *Litsea* in mature and semi-coastal forest. *Myrsine* was a common understory component semi-coastal forest, however less common in the more coastal localities, Atkinson (2004) also noted a stronger presence of *Myrsine* in more sheltered localities. Of the 122 indigenous tree/shrub species identified, only a few were widespread and contributed significantly to the understory of forest, irrespective of site variability. These species included *Geniostoma*, *Brachyglottis repanda*, *Hedycarya aborea*, and *Melicytus ramiflorus.* The ground layer was often sparse, particularly in coastal forest. Characteristically the ground was covered by a dense layer of *Metrosideros* litter and *Adiantium cunninghamii*, *Asplenium polyodon* and *Machaerina sinclairii* were generally the most wide-spread and common ground cover species.

Composition and structure of *Metrosideros* forest located on Moutohora and Tuhua was distinct from that surveyed on the mainland. Isolation from the mainland, disturbance history and the current absence of introduced mammalian pests are likely to in part, explain the distinctness of these islands vegetation. In contrast, *Metrosideros* forest located on Motuotau was more similar to that sampled in areas Kohi Point Reserve, with the exception of two additional species *Melicytus novae-zelandiae* and *Asplenium haurakiense*; both common species of coastal islands.

3.5.2 Comparison with east coast *Metrosideros excelsa* forest

The large majority of *Metrosideros* forest east of Opape, in the Bay of Plenty, was privately owned, and as a consequence, not included in this study. However, Regnier et al. (1988) conducted a broad survey of natural areas within the Pukeamaru Ecological District, and in doing so sampled a wide range of *Metrosideros* forest types extant on the East Coast of the Bay of Plenty. Forest types recognised by Regnier et al. (1988) were not unlike those identified in this study, and thus the structure and composition of *Metrosideros* forest identified here, is also likely to represent that of the wider area. Broadly, Regnier et al. (1988) identified three *Metrosideros* forest types; *Metrosideros* forest, *Metrosideros*–(*Beilschmiedia*)–broadleaf forest and *Metrosideros*–*Vitex* forest.

Metrosideros forest identified by Regnier et al. (1988) was generally present on steep hill-slopes or seaward facing cliffs and had a canopy height < 15 m. *Metrosideros* was the dominant canopy species, however *Pseudopanax lessonii* and *Vitex* contributed significantly to the sub-canopy, with both contributing c. 15% of cover there. *Pseudopanax lessonii*, *Rhopalostylis sapida* and *Coprosma macrocarpa* were common in the shrub layer, and all contributed c. 15% to total shrub cover. Thus this forest type was similar in structure to vegetation groups 1 and 2 identified in the present study; both occupied similar locations and had comparable structural profiles, with significant contributions of *Pseudopanax lessonii* in the understory. However, the East Coast forest had a more diverse range of bird dispersed species, and in particular *Corynocarpus* was a more common component of the *Metrosideros* forest there.

The forest types described by Regnier et al. (1988) as *Metrosideros*–(*Beilschmiedia*)–broadleaf forest and *Metrosideros*–*Vitex* forest also shared a number of similarities with semi-coastal forest identified in this study, particularly with vegetation groups 7, 8 and 9. The presence of *Beilschmiedia* and *Dysoxylum* in the canopy was a commonality between forests, as was *Brachyglottis repanda*, *Macropiper excelsum* and *Geniostoma* in the understory and shrub layers. Regnier et al. (1988) also report *Weinmannia* as a significant canopy component (c. 15% cover) in a limited number of semi-coastal *Metrosideros* forests, similarly this survey found *Weinmannia* was common among *Metrosideros* assemblages which occupied landslide and slip scars. There was a strong presence of *Litsea* in the

shrub layer and sub-canopy of semi-coastal forests surveyed in this study; however this was not reported for the East Coast forests. This inconsistency may be exaggerated because Regnier et al. (1988) only reported species present in >50% of quadrats and with >5% cover in a forest tier. However *Litsea*, juveniles in particular, were more frequent than this in the current study. Conversely, *Vitex* and *Corynocarpus* were seemingly much more abundant in the East Coast forest, where they contributed some 23% and 15% canopy cover respectively in the quadrats described.

3.5.3 National comparison

Metrosideros forest in the Bay of Plenty is structurally similar to that outside of the region, though has a unique combination of species. Little Barrier Island (Hauraki Gulf) is considered to host some of the most extensive and intact *Metrosideros* forest remaining in New Zealand (Bergin & Hoskings 2006). Hamilton & Atkinson (1961) broadly describe *Metrosideros* forest on the island as either coastal *Metrosideros* forest or semi-coastal *Metrosideros*/broad–leaved forest. Coastal *Metrosideros* forest on Little Barrier Island is somewhat analogous to vegetation groups 1, 2 and 5 identified in this study. Similarly the forests occurred on coastal cliffs, headlands and valley mouths and were structurally very similar; both are characterised by a c. 15 m *Metrosideros* dominated canopy, accompanied by other coastal species such as *Pseudopanax lessonii*, *Coprosma lucida*, *Coprosma robusta*, *Macropiper excelsum*, *Pittosporum crassifolium* in the understory. However the floristic composition did differ between the two regions, Great Barrier Island had a seemingly richer flora, and a strong presence of *Planchonella costata* (tawapou); a species whose recruitment in hindered in the presence of rats (Campbell & Atkinson 1999) and less common in mainland forests. Hamilton & Atkinson (1961) also noted the abundance of *Entelea arborescens* and *Myoporum laetum*; neither species was present within Bay of Plenty mainland quadrats, however they were common within *Metrosideros* forest sampled on Moutohora.

Similar to that in the Bay of Plenty, semi coastal *Metrosideros*/broad–leaved forest on Little Barrier Island (Hamilton & Atkinson 1961) also represented a transition in forest types, between coastal forest and lowland forest (predominantly *Beilschmiedia tawa*). This vegetation type is comparable with

vegetation groups 9 and 7 identified in this study, sharing many species and having a similar structural profile. In both regions, *Metrosideros* dominated the canopy, with *Beilschmiedia* and *Dysoxylum* also making notable contributions, but contributing more significantly to the understory and sub-canopy layers. Other common species in the understory in both regions include *Litsea*, *Corynocarpus*, *Pseudopanax arboreus*, *Geniostoma rupestre*, *Brachyglottis repanda*, *Schefflera digitata* and *Macropiper excelsum*. Hamilton & Atkinson (1961) also noted the presence of *Rhopalostylis sapida* assemblages in damper regions of *Metrosideros* forest, and these too are present in the Bay of Plenty forests, particularly within Ohope Scenic Reserve (Figure 3.13).

Figure 3.13: Photograph of a *Rhapalostylis sapida* grove within *Metrosideros excelsa* forest, Ohope Scenic Reserve.

Metrosideros forest surveyed on Great Barrier Island covered both semi-coastal and coastal forest stands, and forests did not vary greatly from those surveyed in the Bay of Plenty, or those on Little Barrier Island. Two additional tree species were present in the semi-coastal forest, which were not found in the equivalent, Bay of Plenty sites. These were *Beilschmiedia tarairi* and *Metrosideros robusta*. The Bay of Plenty is within both species natural distributions, however *Metrosideros robusta* is more common in the upland areas with richer soils, and *Beilschmiedia tarairi* is more common in the northern parts of the East Cape (Dawson and Lucas 2011). Coastal forest surveyed on Great Barrier was analogous with Bay of Plenty stands in forest type 2. This represented coastally exposed sites, in an early phase of forest development, and it is likely similarities

are a result of the site conditions limiting forest composition to species that are tolerant of exposure to strong salt laden winds.

Bellingham et al. (1999) present species richness, total tree density and total basal area (trees >10cm dbh) for 14 spatially extensive forests around New Zealand, predominantly *Nothofagus* forest and mixed *Nothofagus*–hardwood forests. Comparison of species richness figures (trees m^{-2}) for the 14 forests, with species richness within *Metrosideros* forests, suggests *Metrosideros* forest richness is highly variable between sites, however on average, lower maybe lower than forest types elsewhere (4 cf. 3.6). Forests reported by Bellingham et al. (1999) with fewer than four tree species per 400 m^2 were predominantly at elevations exceeding 900 metres, and species richness in New Zealand is known to decline with increasing altitude (Wardle 1991). No forests included in Bellingham et al. (1999) analyses were within the coastal zone. Comparison of tree density and basal area figures with those in the current study also indicates the high variability within *Metrosideros* stands; the variation between *Metrosideros* forests was greater than the variation between forest types reported by Bellingham et al. (1999). However, in general *Metrosideros* forests may have lower densities (5–43 cf. 16–46.3), particularly mature stands. Tree basal area of *Metrosideros* forests had a much wider range than that reported by Bellingham et al. (1999) (1.47–3.03 cf. 0.8–4.5); again emphasising the high variability between *Metrosideros* stands.

3.5.4 Conclusion

The rarity and limited extent of *Metrosideros* forests has resulted in the forest type being left out of nationwide forest classification schemes. Thus this research presents new quantitative data which describes the current composition and structure of *Metrosideros* forests in the Bay of Plenty. *Metrosideros* forests are a conspicuous component of the coastal landscape in the region and are of high ecological significance. Although forests only represent approximately 10% of their former distribution, they showed an intricate and varied vegetation pattern. Variation between *Metrosideros* forests was largely due to understory species diversity, and this was correlated with location, topography, management and forest age. Overall species richness within sampled *Metrosideros* forests was low in comparison to other indigenous forest types; however semi-coastal and mature forests hosted a more diverse understory than coastal forest. *Metrosideros* forests

in the Bay of Plenty were not unlike those found in other regions, although did host a different combination of species, particularly in semi-coastal locations.

Chapter Four: Autecology of *Metrosideros excelsa* and key forest associates

4.1 Introduction

Species life-history differences, such as growth rates, survivorship, longevity and tree size are important when considering species co-existence in forest communities and compositional shifts through time (Lusk & Smith 1998). Species coexistence and successional replacement is commonly explained by interspecific niche differences expressed during regeneration, this may include species substrate preferences and differential responses of juveniles to light gradients in the forest understory (Lusk 1995; Lusk & Smith 1998).

Light availability is generally considered the primary determinant of spatial and temporal patterns of tree recruitment in forests (Kitajima 1994). Accordingly, species can be ranked along an arbitrary axis, with high growth rates and high light requirements at one extreme and low growth rates and shade tolerance at the other (Kitajima 1994). Shade tolerance is associated with a wide range of plant traits, with different suites of these having effect at different phases of ontogeny. For example, seedling growth and performance is largely effected by seed reserves (Walter & Reich 2000); shade-tolerant species tend to have large seeds and storage cotyledons, while light demanding species tend to have small seeds and photosynthetic cotyledons (Kitajima 1996). Generally, larger seeded species can establish more readily over a range of conditions owing to a longer period of support by seed reserves, while smaller seeded species are more often reliant on disturbance (Burke & Grime 1996); such is the case with *Metrosideros*. Although one study (Wotherspoon 1993) has investigated the regeneration ecology of *Metrosideros excelsa*, it did not examine the species' specific light requirements (shade tolerance) or life history traits from juvenile phases through to maturity.

4.2 Aims and objectives

Structure and composition of *Metrosideros* forest is directly dependant on the establishment and persistence of *Metrosideros* and of secondary species beneath the closed canopy, thus the objective of this research is to examine key life history

traits of *Metrosideros excelsa* and associated species, particularly juveniles' shade tolerance variations. The specific aims of this chapter are:

(1) Quantify the light environments occupied by juvenile *Metrosideros* and associated species, to determine the relationship between species regeneration strategies and shade tolerance;

(2) Quantify growth performance variations between *Metrosideros* and key canopy species *Litsea* and *Beilschmiedia*, under different light regimes;

(3) Determine the longevity of *Metrosideros* individuals and deduce a diameter age relationship to allow age estimates to be made for Bay of Plenty forests.

4.3 Methodology and analysis

4.3.1 Deducing diameter age relationships

Diameter increment data from stem disks were combined with the Clarkson & Clarkson (1991) data set. The relationship between stem diameter and tree age was determined by fitting the data with the Gompertz function (Ratkowsky 1983) diameter = A.exp (-exp (- B (Age-C))), where A, B and C are fitted parameters. The Gompertz function was chosen as it is a mathematical time series model, often used in ecological studies to predict diameter-age relationships (Erickson 1976). Diameter increment data was also obtained from permanent quadrat re-measurements. Differences between annual stem diameter increments and sites were investigated using Analysis of Variance (ANOVA) and *a posteriori* (post-hoc) LSD tests. The assumption of homogeneity of variance was assessed using the Levene's test and the condition of normally distributed data was verified using the Sharpiro-Wilk test.

The Gompertz relationship between stem diameter and age was used to predict the forest age within each quadrat, based on the diameter class which contained the largest number of *Metrosideros* stems (modal size class). Because *Metrosideros* characteristically establishes on open sites following a disturbance event, the age of the most frequently occurring stem size (modal size class) is considered to be

analogous with stand age. Error is likely to occur when extrapolating beyond the range of the data set; thus quadrats with a modal diameter size class greater than 100 cm were considered to be 300 years or greater, and were not denoted with a specific stand age.

4.3.2 Species distribution in relation to canopy openness

Hemispherical photography was used to compare and contrast the light environments naturally occupied by juveniles of *Metrosideros*, *Litsea*, and *Beilschmiedia*. Ten transects of variable length (70–60 m) and running at a constant bearing were positioned within three of the study sites, these were Ohope Scenic Reserve, Matata Scenic Reserve and Kohi Point Reserve. Transects were systematically placed to cover stream terraces, hill-slopes, gullies and ridges, thus covering the full range of forest floor and light environments available within the study sites.

Sampling points were spaced at random intervals (5–15 m apart) along transects. At each sampling point the nearest two species of interest with heights between 15 cm and 150 cm were located and their height, diameter (at 10 cm above ground height) and leaf number was recorded. Juvenile height was measured to the nearest millimetre and measurements were taken from the base, or above any adventitious roots in the case of *Metrosideros*, to the top of the apical bud. If the juvenile had more than one leading shoot the tallest was always measured. Diameter measurements were made using digital callipers on the main stem, 100 mm above the stem base. To improve accuracy, two measurements were taken at perpendicular angles across the stem and measurements were recorded to the nearest hundredth of a millimetre. Juveniles were emitted from the study if they displayed severe leaf of stem damage.

Hemispherical photography using a digital camera (Nikon Coolpix995) adapted with a hemispherical fish eye lens (FC-E8) was used to capture the light environment occupied by each juvenile. Photographs were taken on overcast days or at dawn and dusk as this ensured uniform sky conditions. Camera exposure was set at 2 F-stops above a meter reading on open sky, to guarantee over exposure. Photographs were taken directly above the juveniles apices using an adjustable tripod, the camera was always level and aligned to the north with the lens orientated vertically upward. In addition to the photographs taken above juveniles,

further photographs were taken to determine the overall distribution of light environments within the forests; these were taken at random intervals (2–20 m apart) along the forest transects with camera positioned 100 cm above the ground. To determine the light environment occupancy of common understory associates, the presence or absence all other species present in a 1 m radius was also recoded along one Ohope and one Matata transect.

4.3.3 Growth performance

Hemispherical photography was also used to examine shade tolerance and growth performance variation between seedlings and small saplings of *Metrosideros, litsea* and *Beilschmiedia*. In March 2011, 40 individuals of each species were randomly located along four forest transects (Ohope Scenic Reserve, Matata Scenic Reserve); transects were of variable length (50–100 m) and covered terrace, gully and hillslope vegetation. Juveniles were tagged and located with a Global Positioning System (GPS), to allow relocation. Initial height, diameter (100 mm from base) and leaf number were recorded for each juvenile, following the same procedure as outlined above. Relocation and re-measurement of all juveniles, with the exception of one *Litsea* juvenile, suspected to have died, occurred in late October 2011; capturing eight months of growth.

At the time of relocation, hemispherical photography using a digital camera (Nikon Coolpix995) adapted with hemispherical fish eye lens (FC-E8) was used to capture the light environment occupied by each juvenile; allowing the examination of growth performance and light environment relationships. Photographs were taken following the same procedure outlined in section 4.2.3 above.

4.3.4 Light environment occupancy and growth performance

Gap Light Analyser software (Version 9.0) was used to analyse hemispherical photographs. Percentage of canopy openness was the parameter used to deduce the understory light environments occupied by species. Interspecific differences between the understory light environments occupied and interspecific growth performance, were investigated using Analysis of Variance (ANOVA) and *a posteriori* LSD tests; the assumption of homogeneity of variance was assessed using the Levene's test and the condition of normally distributed data was verified

using the Sharpiro-Wilk test. Assumptions were ignored when the sample size was >30, as per the central limit theorem. Juvenile's relative growth rates (RGR) were calculated using:

Height growth = Log_e Height (T2) - Log_e Height (T1) / time (T2-T1)

Diameter growth = Log_e Diameter (T2) - Log_e Diameter (T1) / time (T2-T1)

Where T1= initial measurement, and T2= finial measurement (Burten & Mueller-Dombois 1984).

The geometric mean was used, as opposed to the arithmetic mean, to typify the central tendency of species in respect to the range of light environments occupied. The mean light environment of the forest understory was calculated in the same manner. The geometric mean was used as opposed to the arithmetic mean because the distribution of species and the forest understory light environments were approximately log-normally distributed. Also, the response of juvenile tree growth and survival is more closely related to a log scale of light availability than they are to an arithmetic scale (Poorter 1999; Lusk 2009).

The 10^{th} percentile of the distribution of each species in relation to light environment (percentage of canopy openness) was used to approximate the minimal light levels tolerated by the study species (Lusk et al. 2008). This parameter was calculated for all species that had a samples size >20, and also for *Litsea*, *Metrosideros* and *Beilschmiedia* in three height classes (>30 cm, 30-60 cm, >60 cm). The intraspecific differences in minimum light requirements across the size classes were used as an indication of a species changing light requirements with ontogeny.

4.3.5 Growth rates

Metrosideros growth rates were deduced in two ways; first from the diameter growth of stems in permanent quadrats, divided by the number of years that had passed before re-measurement, and second from ring counts on cut stem disks. Four permanent quadrats were re-measured; three quadrats on Tuhua and one quadrat on Motuotau. *Metrosideros* stems in Tuhua quadrats were not individually tagged, therefore diameter growth increments were presented as average values per sub plot (10 × 10 m). Conversely, all *Metrosideros* trees were tagged in the

Motuotau quadrat and individual stems were able to be traced, accordingly diameter increments are presented for each tree.

Where possible, growth-ring counts were also made on stem disks, to establish a diameter-age relationship. A total of sixteen stem disks were sourced from fallen trees at Matata, Ohope and Kohi point. Stem discs were prepared by sanding back the roughly sawn sections with sequentially finer grades of sandpaper until a smooth finish was achieved. Disks were then oiled with linseed oil to emphasise the distinction between the late and early wood. Growth rings, although described by Meylan and Butterfield (1978) as indistinct to slightly distinct, were clearly visible and able to be counted with the aid of a binocular microscope. For the purpose of this study, it is assumed a single ring equates to a single year's growth. However further investigation is needed to determine whether *Metrosideros* is capable of producing multiple growth rings per year, like other New Zealand species which occupy the same warm temperate climatic region (Bergin & Hosking 2006).

4.4 Results

4.4.1 Species light environment distributions

Forest understory and species light environment occupancies are illustrated on Figure 4.1. Sampled understory light environments ranged from 0.13% canopy openness with a corresponding total light transmittance of 0.1% (observed in Ohope Scenic Reserve), to 44.2% canopy openness with a corresponding total light transmittance of 72.15% (Matata Scenic Reserve). There was a highly significant difference between species and light environment occupancy (F = 46.12; d.f = 2; $P < 0.001$); characterized by the percentage of canopy openness directly above juvenile apices. The distribution of light environments occupied by *Metrosideros*, *Kunzea*, *Litsea*, *Beilschmiedia*, *Dysoxylum* and *Corynocarpus* juveniles all differed significantly from the distribution of light environments available in the forest understory (P <0.001). Conversely, the distribution of light environments occupied by the species *Hedycarya*, *P. arboreus*, *Geniostoma* and *Myrsine* did not differ significantly from the randomly sampled forest understory (P = 0.114, 0.167, 0.029, 0.290 respectively).

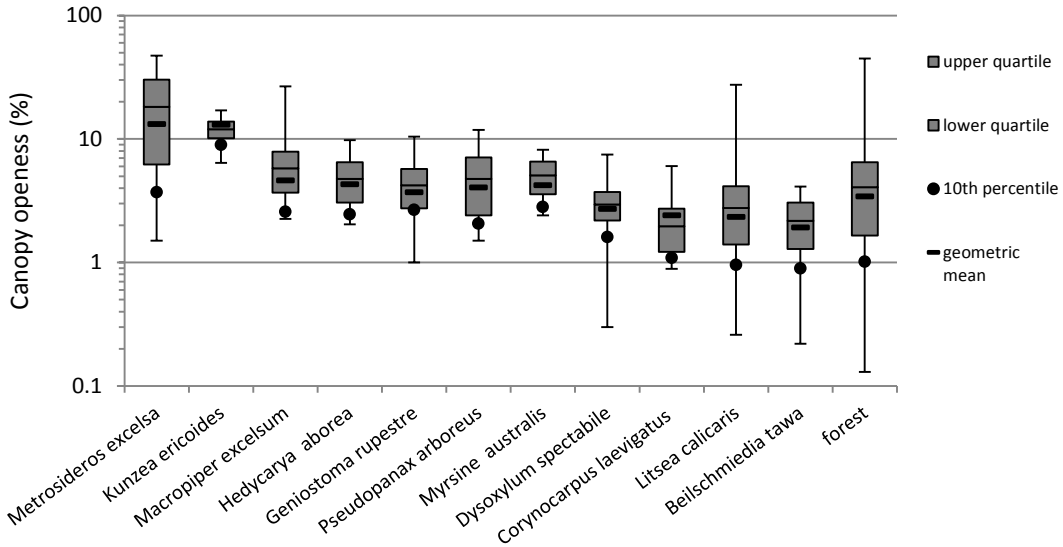


Figure 4.1: Minimum value, maximum value, geometric mean, upper and lower quartile and 10th percentile of light environments occupied by species juviniles.

4.4.2 Interspecific shade tolerance variation

Beilschmiedia had the lowest minimum light requirement of all species sampled (estimated from the 10th percentile of light environments occupied), followed by *Litsea*, *Corynocarpus* and *Dysoxylum* (0.88%, 0.95%, 1.08% and 1.80% of canopy openness, respectively). The geometric mean of the light environments occupied by these species (1.91%, 2.33%, 2.71%, 2.90% canopy openness, respectively) were all below that of the forest understory (3.40% canopy openness), suggesting these species juveniles showed bias towards the lower light environments available. This result is consistent with the species sequence as secondary immigrants in *Metrosideros* forest successions, identified by Atkinson (1994) on New Zealand's northern offshore islands. Conversely, *Kunzea* and *Metrosideros* juveniles had the highest minimum light requirements of sampled species (8.94% and 3.68% of canopy openness, respectively). The minimum light requirements of these two species were well above that of the forest understory, thus confirming their status as shade intolerant species (Hosking 2006; Atkinson 2004).

Of the understory species which did not have a statistically significant different light environment occupancy to the randomly sampled forest understory, *Macropiper excelsum* and *Hedycarya aborea* tended to show a slight bias toward higher light environments, whereas the geometric mean of the light environments occupied by *Geniostoma rupestre* and *Myrsine* were close to that of the forest understory.

The light environments occupied by frequently occurring species (n >20) were approximately log-normally distributed. Log-normal light environment distributions of *Litsea*, *Dysoxylum* and *Beilschmiedia* juveniles and the forest understory (Figure 4.2), were centred on 1%–4% of canopy openness, whereas that *Metrosideros* was centred on 16%–32% of canopy openness; emphasising the markedly different light preferences between *Metrosideros* and the later successional tree species.

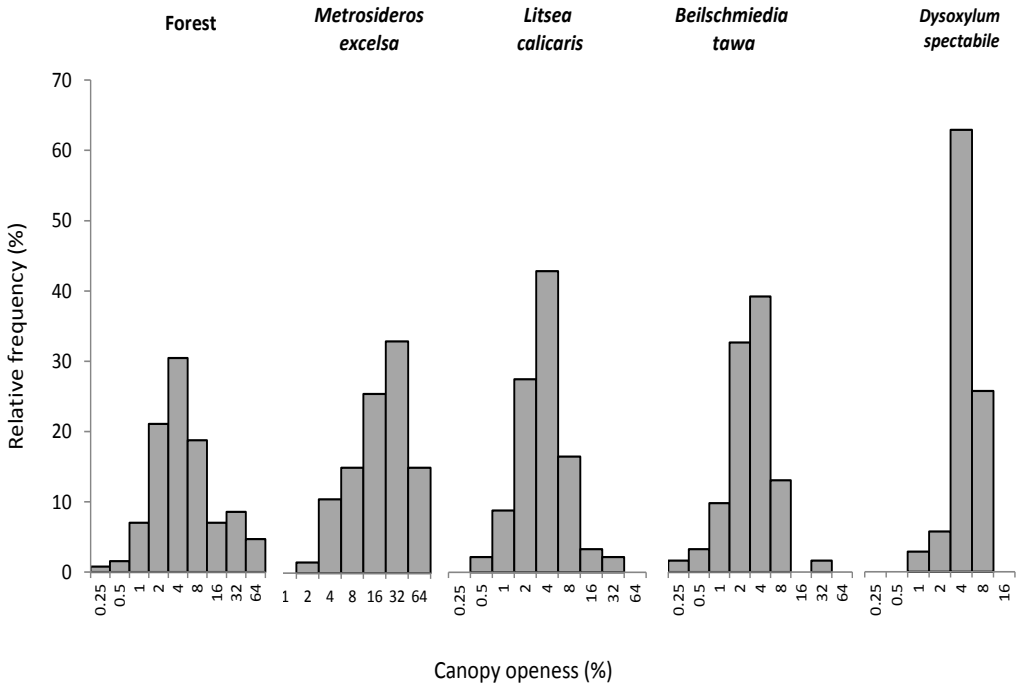


Figure 4.2: Relative frequency distributions of light environments occupied by juveniles of four canopy species present in *Metrosideros excelsa* forest development. 'Forest' illustrates the distribution of a random sample of light environments.

4.4.3 Ontogenetic changes in minimum light requirements

The minimum light requirements of these three species showed ontogenetic variation; minimum light requirements of *Metrosideros* juveniles significantly decreased with increasing juvenile height, across all three size classes (P = <0.0001), whereas those of the later successional species, *Litsea* and *Beilschmiedia* both showed a slight increase across increasing juvenile height classes, however increases were not significant (*Litsea* P= 0.99, 0.41 respectively; *Beilschmiedia* P = 0.51, 0.83 respectively). *Litsea* and *Beilschmiedia* juveniles also showed a rank reversal in the 30–60 cm height group, with *Litsea* juveniles occupying lower light environments (Figure 4.3). Interspecific variation between the three species minimum light requirements was wider in the smallest height class (0.287) than in the larger two height class groups (0.256 and 0.146 respectively), suggesting interspecific light requirements of older/taller juveniles may be more similar.

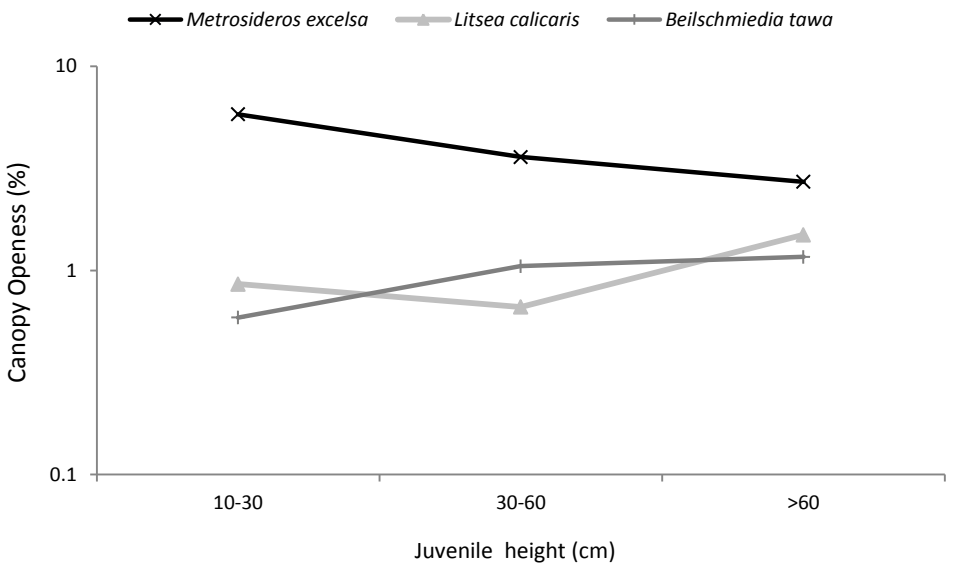


Figure 4.3: Minimum light requirements (10^{th} percentile of canopy openness) of *Metrosideros excelsa*, *Litsea calicaris* and *Beilschmiedia tawa* juveniles across height classes.

Examination of *Metrosideros*, *Dysoxylum* and *Litsea* juveniles diameter and height relationships has revealed moderate-strong positive associations (r^2 = 0.75, 0.57, 0.87 respectively), the lower correlation between *Litsea* juveniles heights and diameters was a result of the species having short and stout structure in some cases, particularly in light environments below the species geometric mean of canopy openness (Figure 4.4). This may suggest *Litsea* juveniles are able to survive in light levels below their optimum and in such cases, juveniles may allocate biomass to stem width rather than increasing stem height. In a randomised experiment where *Litsea* juveniles where grown under differing light availability, juveniles grown in c. 40% of full light had 2 times higher relative height growth rates than those grown in 2% of full light, conversely diameter growth rates were not significantly different (R.J Bylsma unpubl. data). This is consistent with previous research conducted by Smale & Kimberley (1983), which suggests *Litsea* is reliant on light gap formation before juveniles are able to mature and contribute to canopy foliage.

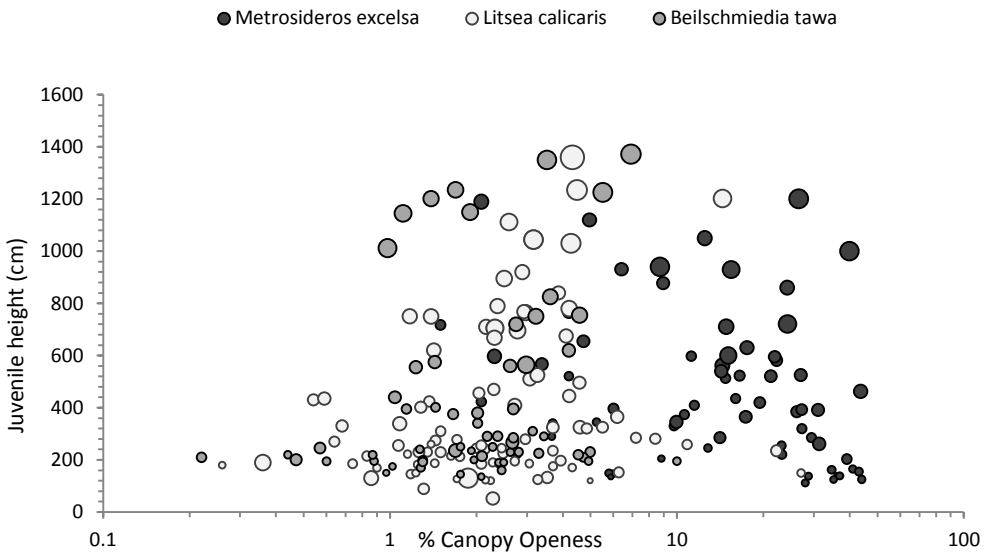


Figure 4.4: Height (mm), diameter (mm) and light environment (% canopy openness) for *Metrosideros excelsa*, *Litsea calicaris* and *Beilschmiedia tawa* juveniles. Stem sizes are proportionally scaled, with the largest stem equal to 17 mm.

4.4.4 Interspecific growth variation

Examination of species relative growth performance along a gradient from high to low light did highlight interspecific variations. The average height RGR of *Litsea* juveniles was higher than those of *Beilschmiedia* and *Metrosideros* (0.52, 0.31, 0.29 mm.mm year^{-1}, respectively); two *Litsea* juveniles in particular had accelerated growth rates compared to other *Litsea* juveniles sampled, and these were growing under dense canopies with 1.29% and 1.6% of canopy openness. The relative height growth *Metrosideros* juveniles reached maximum rates in locations where there was between 14% and 22% of canopy openness. A number of *Metrosideros* juveniles also appeared to have negative growth rates. If a juvenile had more than one shoot, the tallest was always measured and this resulted in an underestimate of growth in some individuals when the tallest shoot was not actively growing, thus negative growth are not included in this analysis. The relative height growth of *Beilschmiedia* juveniles peaked between 1.9% and 2.79% of canopy openness. The relative diameter growth of *Metrosideros* and *Beilschmiedia* mirrored that of their height growth along an axis of high of low light. However relative diameter increases of *Litsea* juveniles were generally consistent in both high and low light; thus again confirming the notion that *Litsea* juveniles allocate biomass to stem width, rather height under low light levels.

Based on species juvenile's minimum light requirements and growth performance, *Metrosideros* and associated canopy tree species had the following order of shade tolerance:

Beilschmiedia>Litsea>Dysoxylum=Corynocarpus>Metrosideros>Kunzea.

Percentage of Canopy openness has been used to characterise juveniles light environments, however this parameter does not take solar tracks into account or distinguish between the north and south sides of canopy gaps, which may differ considerably in direct irradiance (Lusk 2009). However, when total light transmittance (a parameter also calculated in GLA ver. 9.0) was used as opposed to percentage canopy openness, juveniles rank order of shade tolerance did not vary from that presented.

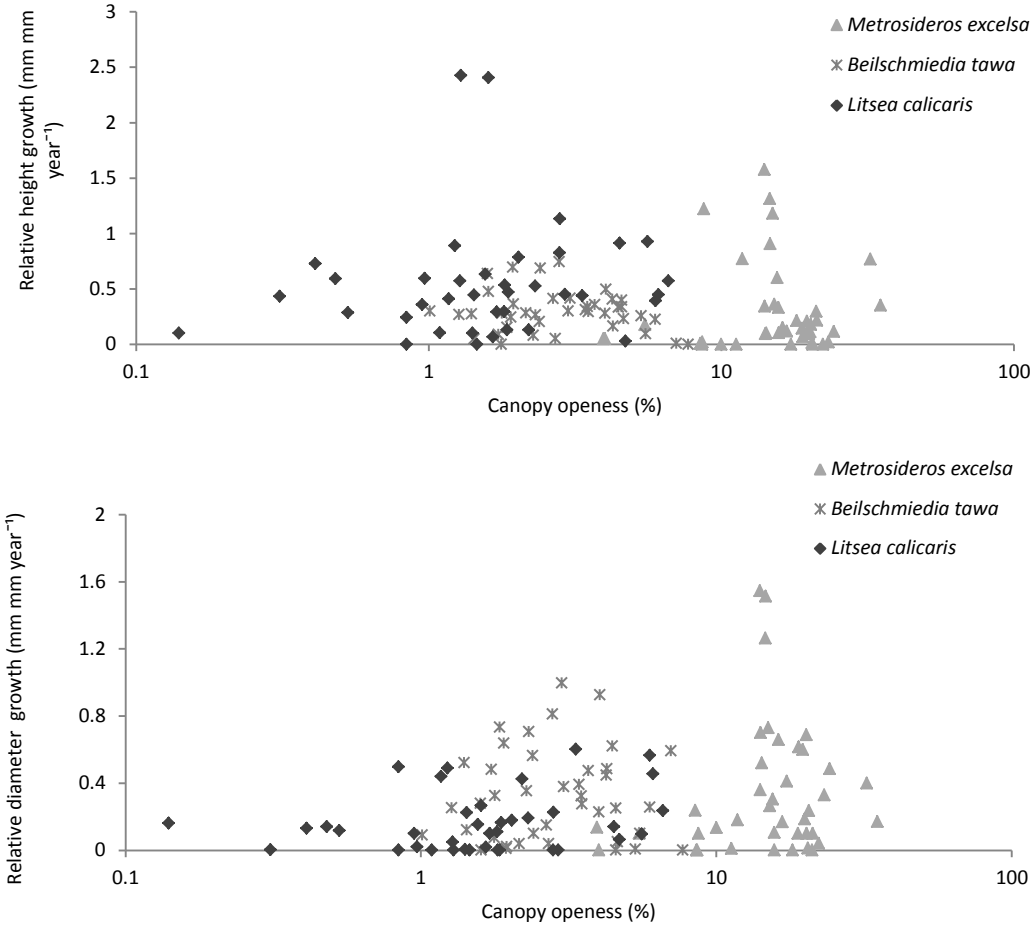


Figure 4.5: (a) Relative height growth (mm mm year^{-1}) (b) Relative diameter growth (mm mm year^{-1}) in relation to canopy openness, of *Metrosideros excelsa*, *Litsea calicaris* and *Beilschmiedia tawa* juveniles.

4.4.5 *Metrosideros excelsa* growth rates

Tuhua

Permanent quadrats on were re-measured 18 years after installation. During this time a considerable number of *Metrosideros* stems died; these dead stems were not used to deduce annual diameter growth increments as many would have decreased in diameter due to the decay of dead wood. *Metrosideros* stems ranged from 3.3–110.7 cm dbh in 1990, and this increased to 14.0–114.0 cm dbh at the 2009 re-measurement. Annual stem increments within subplots ranged from 0.24–2.69 cm year^{-1}; stem increments were generally higher in the quadrat located at South East Bay, where *Metrosideros* stems were considerably larger and therefore considered older.

Table 4.1: Average diameter growth increments of *Metrosideros excelsa* stems in permanent quadrats on Tuhua, 1990–2009.

		Average diameter (cm)		Increment (cm year^{-1})	
Quadrat identifier	**Subplot**	**1991**	**2009**	**Subplot**	**Plot**
Panui Peninsula	a	25.91	30.18	0.24	
	b	28.88	42.60	0.76	
	c	24.37	40.70	0.91	
	d	33.29	37.60	0.24	**0.54**
South East Bay	a	47.18	59.20	0.67	
	b	56.65	105.13	2.69	
	c	43.80	59.25	0.86	
	d	58.97	66.48	0.42	**1.16**
Tikitikinahoa	a	18.27	46.00	1.54	
	b	27.68	34.64	0.39	**0.96**

Motuotau

The permanent quadrat on Motuotau was re-measured 21 years after installation. All *Metrosideros* stem diameters were directly compared to their original size (Table 4.2). Stem diameters ranged from 15.8–49.2 cm dbh in 1990 and 14.8–54.5 cm dbh in 2011; the slight decrease in minimum stem size is due to the deterioration of dead wood. The majority of stems increased in diameter by c. 3 cm over the re-measurement period, however some stems showed no growth, whilst several decreased in size. The average annual diameter increments, per *Metrosideros* tree, ranged from 0.09–0.45 cm year^{-1} and were generally much lower than those determined for the Tuhua quadrats.

Table 4.2: Diameter growth increments of *Metrosideros excelsa* stems, Motuotau permanent quadrat 1990–1022.

***Metrosideros excelsa* trees**	**Stem diameter (cm)**		**Increment (cm year^{-1})**	
	1990	**2011**	**Stem**	**Tree**
1	33.1	39.7	0.31	0.14
	21.7	20.8	-0.04	
	23.9	21.0	-0.14	
	23.8	26.5	0.13	
	33.8	41.0	0.34	
	24.1	28.9	0.23	
2	27.9	32.1	0.20	0.09
	27.3	27.7	0.02	
	22.7	23.5	0.04	
3	33.3	37.5	0.20	0.18
	25.2	28.4	0.15	
	24.9	28.6	0.18	
4	30.5	37.4	0.33	0.29
	49.2	54.5	0.25	
5	42.0	44.9	0.14	0.15
	47.2	51.6	0.21	
	38.1	39.8	0.08	
	39.6	42.8	0.15	
6	36.2	36.9	0.03	0.03
7	26.2	28.7	0.12	0.10
	32.0	33.8	0.09	
8	37.4	46.9	0.45	0.45
9	21.0	22.8	0.09	0.09
10	26.8	29.1	0.11	0.11
11	32.3	40.9	0.41	0.08
	27.5	26.9	-0.03	
	30.2	27.1	-0.15	
12	38.0	41.9	0.19	0.19
			Quadrat average =	**0.16**

4.4.6 Stem disks

For the 16 *Metrosideros* stem disks, growth ring counts were conducted. The results were combined with Clarkson & Clarkson's (1994) data set, collectively bringing the sample size to 31. Stem disks had a diameter range of 4.4–44.0 cm and a growth ring range of 17–182 cm. Annual diameter growth increments were calculated (cm $year^{-1}$); giving an average measure of yearly growth over each individual stems life span (Table 4.3). Annual diameter increments of stems ranged from 0.23 cm $year^{-1}$ (Whakaari) to 0.63 cm $year^{-1}$ (Bay of Plenty mainland). There was a highly significant difference between annual diameter increments and sites (ANOVA, F = 44.69; d.f. = 2, 28; $P < 0.001$). Annual diameter increments of stems collected from the Bay of Plenty mainland were significantly larger than those from Whakaari and Moutohora ($P < 0.001$). There was no significant difference between Whakaari and Tuhua annual diameter increments ($P = 0.78$); however the median annual diameter increase of Whakaari stems was lower than that of Tuhua stems (0.27 cm $year^{-1}$ cf. 0.29 cm $year^{-1}$). The diameter growth rates on Whakaari were, as expected, lower than those on the mainland; consistent with the harsh and frequently disturbed environment on the island.

The relationship between stem diameter and growth rings (n) is presented in Figure 4.1. The Gompertz model (Ratowsky 1983) was successfully applied to the data set ($r^2 = 0.87$), with the relationship described by the equation: diameter = A.exp (-exp (- B (Age-C))) where parameters A, B and C are equal to $6.55E^{+16}$, $3.59E^{+00}$ and $1.57E^{-0.3}$ respectively (Figure 4.2). Initially stems had high growth rates, producing annual growth rings which exceeded 0.5 cm. Annual diameter growth rates decreased with increasing stem age; the models suggests stem growth rates begin to plateau after stems reach c. 200 years. The Gompertz model was used to predict the age of study forests which contained *Metrosideros* stems >2 cm dbh. Forest ages within quadrats ranged from 20–>300 years. Two quadrats did not contain *Metrosideros* stems >2cm dbh so the model could not be applied, however the vegetation age of these quadrats was c. 6 years; inferred from the sites disturbance histories. Thus this study surveyed the full range of successional stages within *Metrosideros* forest, from scrub and young developing stands to mature *Metrosideros* forest.

Table 4.3: Diameter and ring counts from 31 *Metrosideros excelsa* stems collected from Tuhua, Whakaari and the Bay of Plenty mainland.

Location	Diameter (cm)	Growth rings (*n*)	Increment (cm year^{-1})
Whakaari	4.4	17	0.26
-Ohauora	4.4	19	0.23
(Clarkson & Clarkson 1994)	5.2	22	0.24
	7.5	22	0.34
	12.1	47	0.26
	13.0	55	0.24
	20.1	64	0.31
	25.0	70	0.36
	25.8	60	0.43
	41.0	141	0.29
Tuhua	11.5	40	0.29
-South East Bay	11.5	45	0.26
(Clarkson & Clarkson 1994)	22.2	58	0.38
	44.0	182	0.24
	37.9	107	0.35
Bay of Plenty	13.5	29	0.47
-mainland	19.4	46	0.42
	15.0	28	0.54
	21.2	38	0.56
	22.9	45	0.51
	26.3	57	0.46
	31.8	65	0.49
	35.7	71	0.50
	28.5	58	0.49
	25.8	51	0.51
	19.2	37	0.52
	17.5	32	0.55
	21.5	53	0.41
	18.2	29	0.63
	19.5	36	0.54
	26.9	61	0.44
Total =	31		

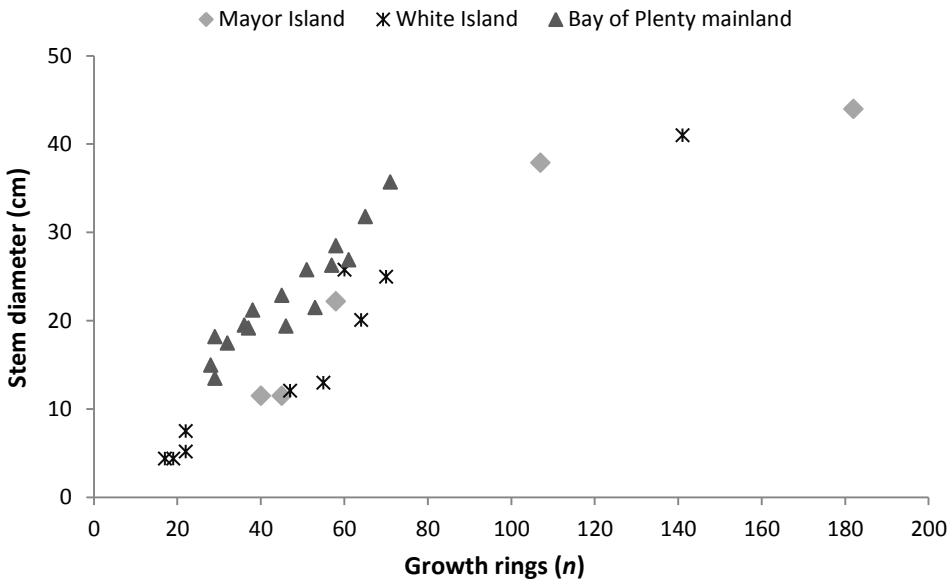


Figure 4.6: Stem diameter (cm) and age relationship, for *Metrosideros excelsa* stems disks, Tuhua (Mayor Island) *n*=5, Whakaari (White Island) *n*=10, Bay of Plenty mainland (*n*=16).

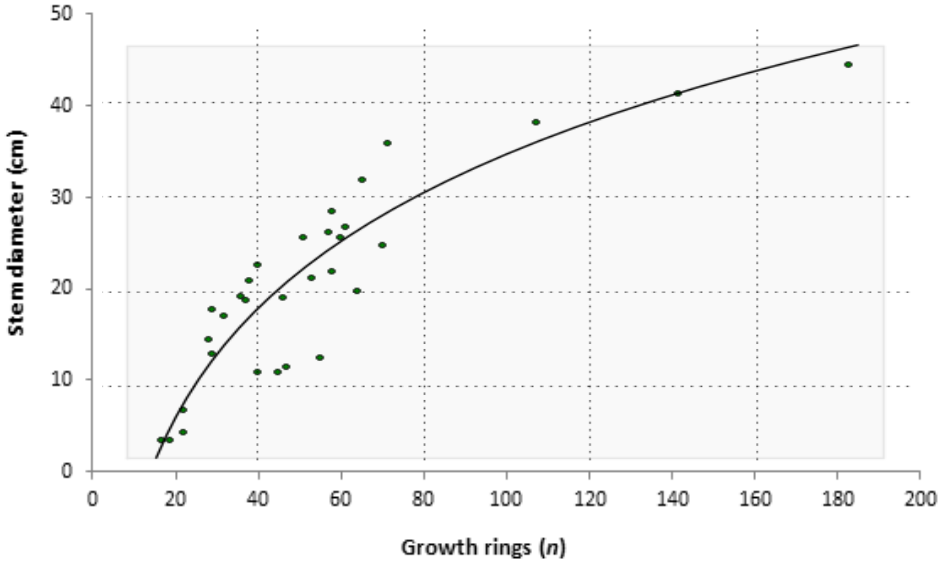


Figure 4.7: Gompertz model of stem diameter (cm) and age relationship, for *Metrosideros excelsa* stem disks, Tuhua (Mayor Island) *n*=5, Whakaari (White Island) *n*=10, Bay of Plenty mainland (*n*=16).

4.4.7 Stand development and dynamics

Figure 4.3 illustrates the decline in *Metrosideros* stem density as forest develops, and allows the rate of self-thinning to be deduced. *Metrosideros* stems decline from >2000–<400 stems ha^{-1} over a developing period of c. 300 years. Basal area of *Metrosideros* stems increased from <20 m^2 ha^{-1} to an average of 50 m^2 ha^{-1} in the first 70 years of forest development, and did not noticeably increase thereafter (Figure 4.4). Plateauing of basal area values at this time is likely to be a result of the diameter increase of live stems balancing those lost to natural self-thinning processes. *Metrosideros* forest also increases canopy height during development, form scrub <2 m tall, to young forest c. 13 m tall and eventually to mature forest which rarely had canopies >20 m in height. In the Bay of Plenty this relationship is confounded by forest location; gully sites generally had taller canopies than ridge of hilltop sites and forest exposed to the sea always had a shorter canopy than equivalently aged sites, inland.

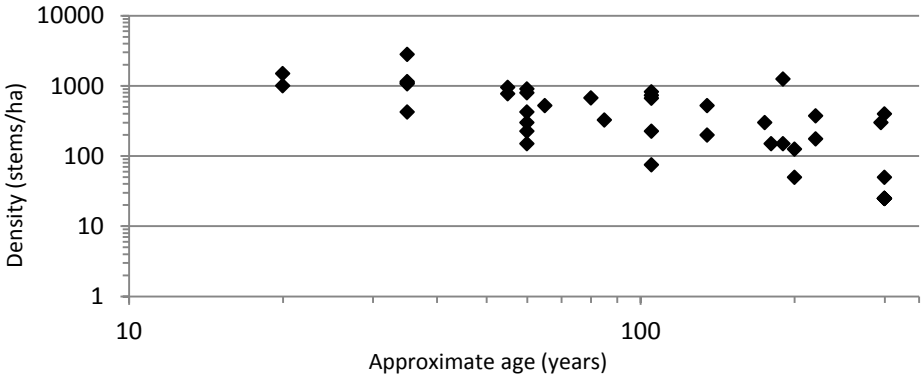


Figure 4.8: Density versus approximate age of *Metrosideros excelsa* stands in in 39 quadrats, including re-measurement data from four permanent quadrats. Both axis are log_{10} scaled.

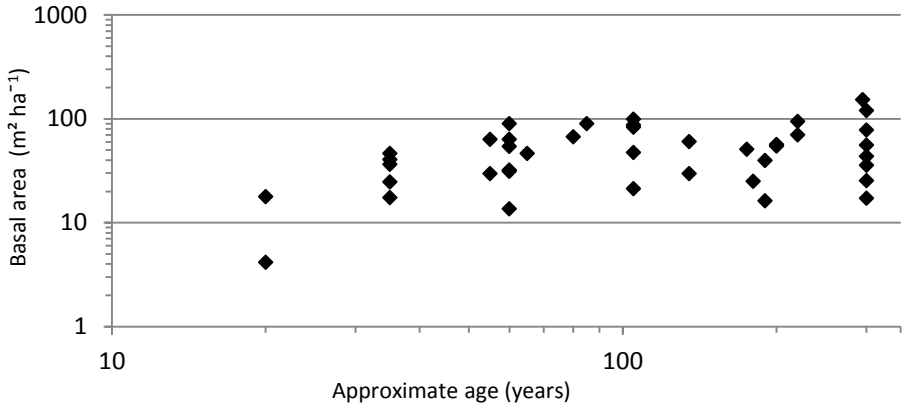


Figure 4.9: Basal area versus approximate age of *Metrosideros excelsa* stands in in 39 quadrats, including re-measurement data from four permanent quadrats. Both axis are log_{10} scaled.

4.5 Discussion

Results of this survey suggest *Metrosideros* juveniles are uncommon in the Bay of Plenty; only being observed in substantial numbers on the coastal banks of Moutohora and along disturbed stream terraces in Matata Scenic Reserve. During a survey of *Metrosideros* health in 1989, a lack of regeneration was noted, and this led to the species being considered threatened with extinction in some regions, particularly the west coast, where dying stands were not being replaced (Forest Research Institute 1989). Many Bay of Plenty reserves are subject to pest control, thus the lack of recent landscape-scale disturbances, rather than the effects of introduced mammalian pests, is likely the reason *Metrosideros* juveniles are currently uncommon (Wotherspoon 1993; Bergin & Hosking 2006).

4.5.1 Shade tolerance

The mean understory diffuse light availability in mature forest was 3.88% (2.64% canopy openness); this is substantially higher than Lusk et al. (2009) found in an old-growth podocarp-broadleaved forest, New Zealand (1.5%). *Metrosideros* juveniles sampled had a minimum light requirement of 3.68% canopy openness, with the exception of *Kunzea*, *Metrosideros* had the highest light requirements of all species sampled. All *Metrosideros* juveniles observed were growing upon hard fissured substrates. Landslides and tree falls often created canopy gaps within *Metrosideros* forest, producing ideal light environments; however if deep soil was present (> c. 10 cm) no *Metrosideros* were observed, instead thickets of *Hebe stricta* and *Coprosma robusta* were common (pers. obs.). The minimum light requirement of *Metrosideros* appeared to show ontogenetic variation, with taller (assumed to be older) individuals having significantly lower light requirements than smaller individuals. Ontogenetic variation in juveniles light requirements have been observed for a number of species; however Lusk et al. (2008) found the minimum light requirements of species with low shade tolerance generally increased with increasing juvenile height; the inverse of what was detected here. Thus ontogenetic variation observed for *Metrosideros* juveniles may not indicate an increased tolerance to shade as they develop, but alternatively may be the result of juveniles being over-topped by faster growing species. To test whether this is the case, the long term survival of shaded juveniles will need to monitored.

Tree species *Beilschmiedia*, *Dysoxylum*, *Litsea* and *Corynocarpus* are common canopy associates in *Metrosideros* forest. In contrast to *Metrosideros* juveniles, these species juveniles were considerably more shade-tolerant. *Beilschmiedia* is regarded as extremely shade-tolerant and commonly develops to advanced stages beneath a closed canopy (Smale & Kimberley 1983); accordingly, in the understory of *Metrosideros* forest, *Beilschmiedia* juveniles were better represented in the shadiest microsites. *Dysoxylum* is also capable of continued regeneration (Smale & Kimberley 1983), and consequently is also more copious in mature and undisturbed *Metrosideros* forest. However, in this study *Dysoxylum* showed little bias towards the darker microsites. This result is consistent with the findings of Buddenhagen & Ogden (2003) who found that *Dysoxylum* seedlings had higher growth rates within, and on the edge of canopy gaps, as opposed to in deep shade. Results from the present study and others (Smale & Kimberley 1983) suggest *Litsea* and *Corynocarpus* are less shade tolerant than *Beilschmiedia* and *Dysoxylum* and may require canopy gap formation before juveniles are able to reach maturity. Results from the present study suggest tree species can ranked in the following order of shade tolerance: *Beilschmiedia* > *Dysoxylum* > *Litsea* > *Corynocarpus* > *Metrosideros* > *Kunzea.* This is the consistent with the order that species arrive in forest succession, identified by Atkinson (2004) on the northern offshore islands of New Zealand.

4.5.2 *Metrosideros excelsa* diameter growth rates

The diameter age relationship exhibited by *Metrosideros* stems in Bay of Plenty forests suggests that stems initially have high growth rates (>4 mm year^{-1} on the mainland) in the first 80 years, but when stems exceed 100 years of age, diameter growth subsequently reduces to <2 mm year^{-1}. High diameter growth rates in the initial phases of forest development, compared to stems in mature forest, have been reported for a number of New Zealand's indigenous species, for example *Weinmannia racemosa* and *Griselinia littoralis* (Smale & Smale 2003; Richardson et al. 2009). The majority of *Metrosideros* stems surveyed were <60 cm dbh and are therefore likely to be <200 years old. This is consistent with the regions general disturbance history, suggesting current *Metrosideros* forest has mostly arisen following burning episodes in the 1900s. Based on the diameter age relationship, the relict *Metrosideros* trees encountered in the Matata, Ohope and Kohi Point Reserves with diameters >150 cm dbh are likely to be older than 1000

years. Simpson (1994) also suggests *Metrosideros* trees are capable of reaching 1000 years, although trees at this age may be approaching the end of their life span.

Diameter growth rates calculated from *Metrosideros* stem disks were significantly higher for mainland stems, compared to those determined from Tuhua and Whakaari. The slower growth rates exhibited by trees on Whakaari are expected to be the result of the islands hostile environment, characterised by substantial and on-going volcanic eruptions (Clarkson & Clarkson 1994). Pardy et al. (1992) assessed *Metrosideros* growth rates in planted stands and small groves, finding that the mean diameter growth rate was 9.7 mm $year^{-1}$; well above those observed in the present study. Bergin and Hosking (2006) reported *Metrosideros* diameter growth rates for individually planted trees (>100 years ago) in areas outside the species natural range. Growth rates ranged from 0.9–1.8 mm $year^{-1}$, also higher than those reported here. One explanation may be that plantation sites have more fertile soils compared to the barren and primary substrates which *Metrosideros* forest naturally establishes upon, or that inland plantation sites are less hospitable and subject to less exposure than the natural stands.

4.5.3 Stand development and dynamics

Data from this study supports findings by Clarkson & Clarkson (1994) who suggest mature *Metrosideros* forest is formed within c. 250 years following the forest initiating disturbance. In the Bay of Plenty, stands which exceed 300 years have larger components of mid and late successional, shade tolerant species, such as *Beilschmiedia*, *Litsea* and *Dysoxylum*. Examination of a variety of indigenous forests dominated by a single early colonising species (e.g. *Kunzea*, *Leptospermum*), suggests pioneer tree species are capable reaching a maximum basal area of 30–40 m^2 ha^{-1} (Smale 1993; Smale 1994; Smale et al. 1995; Kimberley unpubl. data 1993). However, *Metrosideros* in the Bay of Plenty forests were generally able to reach this basal area threshold within the first 80 years of forest development, and generally well exceeded this threshold within 180 years of development. In contrast to *Kunzea* and *Leptospermum* successions, mature *Metrosideros* forest requires a substantially longer time period to mature, c. 150 cf. 250 years (Atkinson 1994; Clarkson & Clarkson 1994).

The self-thinning of *Metrosideros* stems is the most prolific in young stands (<180 years), with c. 11% of stems sampled being dead and an equivalent number showing signs of deterioration. The self-thinning process has been well documented for colonist species. Smale (1993) found a 50% reduction in in *Kunzea* stems after 30 years of forest development on Great Barrier Island and these rates are comparable to those in *Metrosideros* forest. Kimberley (1993 unpubl. data.) reported stem density and basal area in a pole stand of *Metrosideros* on Moutohora in 1991. This stand was within close proximity to a quadrat surveyed in this study (2011), which at the time of measurement was estimated to be 35 years old. Approximately 30% of *Metrosideros* stems were dead, and a further c. 16% showed signs of deterioration at the time of this survey. Comparing the figures between the quadrat surveyed in this study and that by Kimberley (1993 unpub.), although not a direct comparison, shows that in the 20 year time frame between surveys, stems may have decreased from c. 8500–4000 stems ha^{-1} (47% reduction), and this was coupled with an increase in basal area from c. 40–50 m^2 ha^{-1} (25% increase).

Whereas self-thinning in young forest involved the loss of entire trees, self-thinning in mature forest generally involved the sequential loss of tree limbs, which slowly eventuates in the demise of the tree. It was not uncommon for mature trees to have more than 50% of their limbs missing, and the loss of a single limb could create a canopy gaps >10 m^2 (pers. obs.). Atkinson (2004) speculated that self-thinning of *Metrosideros* stems in the early phases of forest development has little effect on total *Metrosideros* canopy foliage, as gaps are successively filled by surviving stems; however self-thinning in mature stands is thought to result in a decrease of *Metrosideros* canopy foliage. This is consistent with patterns observed in Bay of Plenty forests. As a result of self-thinning, the density of *Metrosideros* stems in mature forest was low (c. 80 stems ha^{-1}), however individual trees could have a canopy covering c. 250 m^2 and diameters up to 2 metres. Often isolated individual *Metrosideros* remained when the surrounding vegetation had been replaced by shade tolerant species, such as *Beilschmiedia*, *Dysoxylum* and *Litsea* (pers. obs.).

Chapter Five: Forest succession

5.1 Introduction

Forest dynamics and successional pathways within New Zealand's conifer-broadleaf forests have been thoroughly investigated and many successional and regeneration models proposed (Ogden 1985; Ogden and Stewart 1995). However, currently no comparable model describing the population dynamics and successional pathways within *Metrosideros* forest exists. Demographic research, focussed on *Metrosideros* forest structure in the Bay of Plenty, is limited to a single paper (Clarkson & Clarkson 1994), and this is of restricted scope.

The longevity exhibited by *Metrosideros* is an unusual strategy for a pioneer species, and as a result *Metrosideros* dominates forest successions for hundreds of years following colonisation. Because species replacement occurs over a time frame much greater than that of the human life span, quantifying successional trajectories within *Metrosideros* forest is challenging. Determination of *Metrosideros* and associated species modes of regeneration is essential to understanding successional pathways in these forests. Species regeneration strategies can usually be categorised as either catastrophic, gap-phase or continuous (Veblen & Stewart 1980; Ogden 1985). Catastrophic regeneration refers to the establishment of a cohort population directly following large scale disturbances. Gap-phase regeneration refers to the attainment of main canopy stature beneath small-intermediate sized canopy gaps. Continuous regeneration refers to the steady regeneration of highly shade tolerant species beneath intact canopies, resulting in the steady replacement of older dying trees (Veblen & Stewart 1980; Ogden 1985).

For the purpose of this research, succession is considered a directional change in species composition and physiognomy, when climate remains effectively constant (Finegan 1984). Careful interpretation of key species diameter frequency distributions over a range of stand ages, and long term studies are essential to understanding the dynamics and successional pathways within *Metrosideros* forests. However, species arrival and replacement cannot be considered without considering key mechanisms controlling succession, such as interspecific

variation in shade tolerance (Lusk 2004), previously discussed for key species in Chapter Four.

5.2 Aims and objectives

This chapter examines successional trajectories of *Metrosideros* forest, in the Bay of Plenty Region by assessing *Metrosideros* stand dynamics and key species regeneration strategies across a range of forest ages. This research enhances the understanding of the linkages between species shade tolerance, regenerative strategies and successional status. The specific aims of this chapter are:

(1) Determine the regeneration strategies of *Metrosideros* and key forest associates;

(2) Provide a general model which describes the successional trajectory of *Metrosideros* forests in the Bay of Plenty;

(3) Assess whether and to what extent species shade tolerance differences drives succession in *Metrosideros* forest.

5.3 Methodology and data analysis

5.3.1 Vegetation survey

Forest survey data analysed in Chapter Three, is also examined here, however to further investigate *Metrosideros* forest development and dynamics through time, data from the re-measurement of four permanent quadrats, previously established within *Metrosideros* forest (Original data supplied by BD Clarkson), is specifically analysed. Three of these permanent quadrats were located on Tuhua (Mayor Island) and one was located on Motuotau (Motuotau); capturing 18 and 21 years of forest change respectively. Quadrats were 20 × 20 m, with the exception of one 15 × 10 m quadrat on Tuhua. The re-measurement of previously measured individuals was attempted in all cases and the diameter of all stems ≥2 cm dbh recorded. Saplings, seedlings and ground cover species were recorded following the same procedure as the vegetation survey quadrats, outlined in chapter three. For all species, stem density (stems ha^{-1}) and basal area (m^2 ha^{-1}) has been calculated.

5.3.2 Quadrat grouping by age

Quadrats were grouped into four age classes based on their approximated age and the results of multivariate NMS ordination using PC-ORD Ver. 9.0 software (McCune and Mefford 2011). NMS Analysis was conducted on *Metrosideros* diameter size-class data which underwent a general relativisation prior to ordination, whereby the total number of stems per quadrat was equal to one (P=1). To reduce noise in the dataset, all stems greater than 85 cm dbh were grouped in a single diameter size class (>85 cm dbh); this ensured quadrats from mature *Metrosideros* forest, which often contained a single large *Metrosideros* stem were considered more similar. To investigate the relationship between *Metrosideros* population structure and forest development, the joint-plot function in PC-ORD Ver. 9.0 (McCune and Mefford 2010) was used to overlay a vector of stand age. Stand ages were estimated from diameter-age relationships previously discussed in Chapter Four.

5.3.3 Structure and composition

For each age group, stem density (stems ha^{-1}) and basal area ($m^2\ ha^{-1}$) has been calculated for *Metrosideros* and associated species. These data are presented along with standard deviations and relative dominance. A high standard deviation is indicative of a species having high variability among quadrats, within a group. Species which occurred in less than c. 5% of all quadrats had their density and basal area data pooled and listed as 'other'. Diameter size class distributions are presented for *Metrosideros* stems within each age group; stem frequency has been converted to stems ha^{-1}. Similarly, diameter size class distributions are also presented for associated species which displayed clear distributional across the four age groups.

5.4 Results

5.4.1 Quadrat grouping by age

To examine developmental changes in forest structure, Non-metric Multidimensional Scaling (NMS) was used to group quadrats which had similar *Metrosideros* diameter frequency distributions. The data matrix contained *Metrosideros* diameter size-class data for eighteen 5 cm size classes (quadrats were excluded if all *Metrosideros* stems were <2cm dbh). A Monte Carlo test of 500 runs with randomized data indicated the minimum stress of a 2-D solution was lower than would be expected by chance (P = 0.0199). Thus a satisfactory two-dimensional NMS ordination solution was obtained; this had a final stress and instability value of 10.13 and 0.000001, respectively (Figure 5.1a). Each ordination axis represents an independent gradient in *Metrosideros* diameter size-class space. Approximated stand age is expressed as a directional vector, and is strongly positively correlated with axis 1. Axis 1 was able to explain 62% of variance in the data matrix, whilst axis 2 represented an additional 19.5% of variance, thus combined a total of 81.5% of the variation could be explained.

The NMS ordination identified four distinct groups of quadrats, with quadrats within each group having more similar *Metrosideros* population structures than those in neighbouring groups. Groups were strongly associated with forest age and contained quadrats ranging from either 0–60 years, 60–180 years, 180–300 years and those estimated to be 300 years old or greater (Figure 5.1b). Age is a continuous variable thus a number of different age ranges could have been used to group the data. However, the age ranges used here produced very little overlap in the NMS ordination and therefore indicate *Metrosideros* forests are within four distinct phases of forest development and these a continuum from high density young stands, to mature forest, and then to forest where secondary successional species were becoming prominent in the canopy. The 0–60 year old group represents pioneer scrub and establishing *Metrosideros* forest; the 60–180 year old group represents developing forest; the 180–300 year old groups represent mid-late successional forest and the >300 year old group represents mature *Metrosideros* forest.

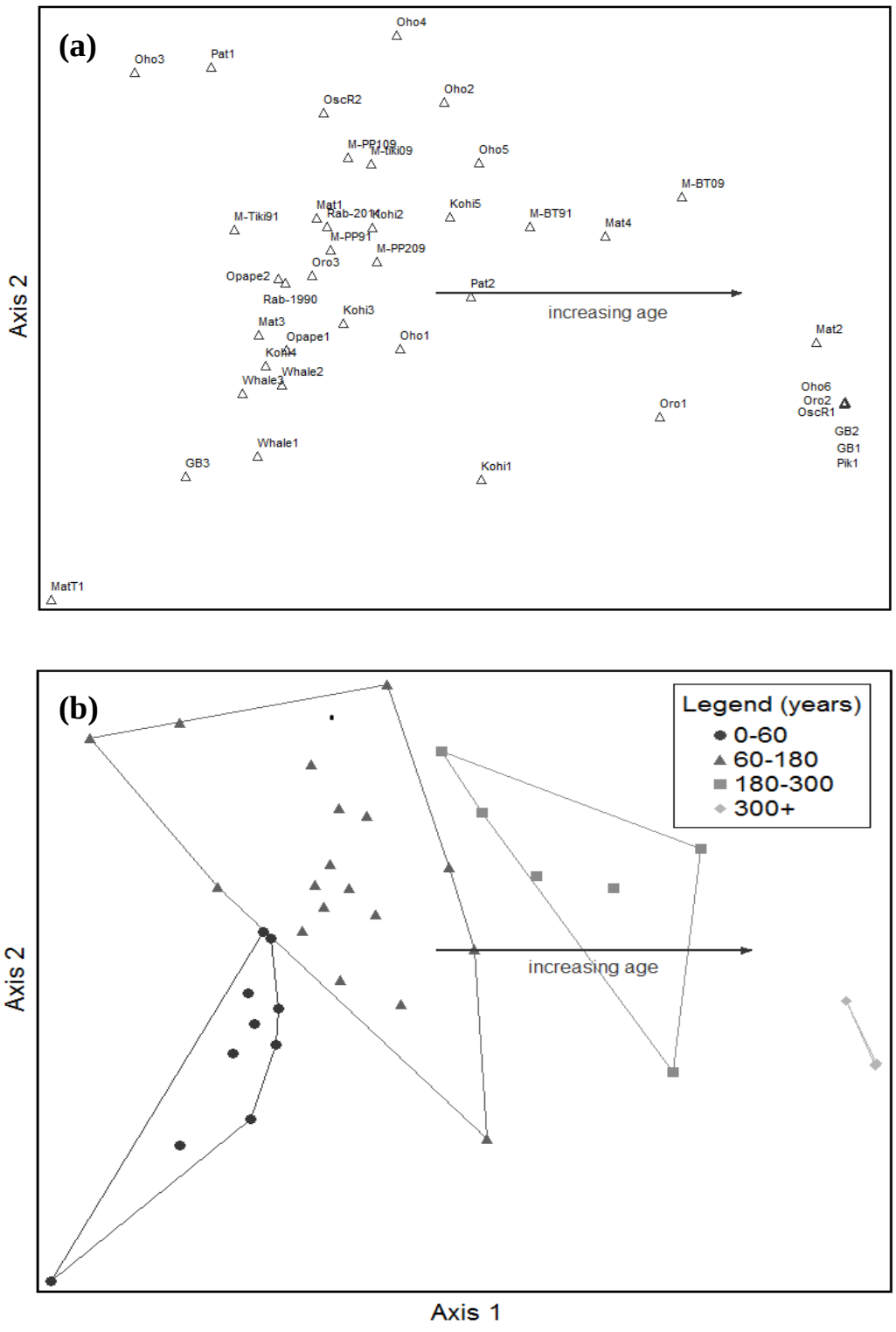


Figure 5.1: (a) NMS ordination of *Metrosideros excelsa* population structure from 39 quadrats (including re-measurement data from four permanent quadrats), located in the Bay of Plenty and Great Barrier Island. **(b)** NMS ordination of *Metrosideros excelsa* population structure with quadrat age groups are shown by solid-line polygons.

5.4.2 Group composition

Compositional changes throughout forest development were assessed by pooling data from a number of different quadrat localities into forest age groups, identified by NMS ordination, and then examining species composite diameter frequency distributions. This technique has previously been criticised because the inference of regeneration strategies from stand structure is based on the assumption that there is a relationship between stem diameter and stem age; pooling data from different sites, with varying soil and climatic variations will invalidate this assumption (Ogden 1978; Stewart & Veblen 1982). However, forest age groups were identified using *Metrosideros* diameter frequency distributions and stand ages were derived from *Metrosideros* stems collected from a wide range of sites in the region. Also, climatic variation in the region is unlikely to be largely different between sites, and thus is not believed to markedly affect the interpretation of diameter frequency distributions.

Table 5.1 and Table 5.2 summarise the floristic composition of *Metrosideros* forest within each of the age groups. *Metrosideros* was the dominant species in all four groups; contributing between 3.1%–28.0% of total density and 63.4%–77.8% of total basal area, across the age groupings. The average density of all stems initially increased with forest age, peaking in the 60–180 year old stands (4875 stems ha^{-1}), and decreasing thereafter (4438 and 2564 stems ha^{-1} respectively). Total basal area also showed a clear relationship with forest age; increasing twofold from 38.8 m^2 ha^{-1} in the 0–60 year old quadrats, to 94.9 m^2 ha^{-1} in the 180–300 stands. These results imply *Metrosideros* forest <180 years old is in a building phase of forest development; gaining in stem density and basal area. The density of standing dead stems ranged from 329 to 36 stems ha^{-1} over the four age groups; rates were greatest in the 0–60 year old stands where self-thinning is most prolific, and decreased thereafter. The total basal area of standing dead stems showed a similar trend, peaking in the 60–180 year old group, and then decreasing; basal area of dead stems ranged from 0.90–1.27 m^2 ha^{-1}.

Group 1: 0–60 years

Metrosideros stems contributed 70.1% of total basal area and 29.5% of total density; generally present in the form of many young stems with diameters ranging from 2.0–42.3 cm dbh. Dead *Metrosideros* stems were also present,

contributing 3.8% of total basal area and 1.5% of the total stem density; often live *Metrosideros* stems had foliage dieback and showed signs of deterioration. No other species contributed more than 10% to the total basal area or total density of this group. However common shrub and understory species included *Kunzea*, *Myrsine*, *C. dealbata*, *Geniostoma* and *M. ramiflorus.*

Group 2: 6–180 years

Metrosideros stems contributed 70.2% of the total basal area and 9.3% of total stem density in this age group. *Metrosideros* stems ranged from 6.2–162 cm dbh, however the majority of stems were between 20–70 cm dbh; larger stems were uncommon and likely to be the result of an earlier colonisation event. The basal area of standing dead *Metrosideros* stems was highest in this group. *Knightia* makes the second largest contribution to total basal area (8.1%), however only contributed a mere 1.7 % to total density. *Knightia* was present as large scattered emergent trees, more common in ridgeline quadrats. Understory species *P. crassifolius* and *C. dealbata* also contributed significantly to total basal area (4.4% and 4.1%, respectively), and *M. australis* and *C. lucida* were present at seemingly high densities (228.0 and 381.3 stems ha^{-1}, respectively), however the latter two were present only in shrub layer and contributed little to the total basal area of the group.

Group 3: 180–300 years

Metrosideros stems contributed 77.8% of the total basal area and 5.2% of total stem density; stems ranged from 12.0–162 cm dbh, however the majority were between 30–80 cm dbh. Larger *Metrosideros* stems were more frequent than the previous group, and again are likely relics of earlier colonisation phases. *Cyathea dealbata* makes the second largest contribution to total basal area (4.5%), followed by *Knightia* (3.4%) and *P. lessonii* (3.1%). Often *C. dealbata* formed tight sub-canopies up to twelve metres tall; directly beneath which, fewer shrub and seedling species were able to grow. Similar to the previous group, *Knightia* had a high basal area coupled with a comparably low density; a result of a few large emergent trees. Other common understory species included *Litsea*, *Hedycarya*, *Geniostoma* and *C. medullaris.*

Group 4: ≥300 years

Metrosideros stems contributed 63.4% of the total basal area and 3.1% of total stem density; these contributions were lower than in the previous three groups, indicating a shift in composition to latter successional species. *Metrosideros* trees had very low densities, often only a single tree was present within a quadrat. *Metrosideros* stems were large, and ranged from 64.5–247 cm dbh, however all but one stem sampled was above 80 cm dbh. No dead *Metrosideros* stems were present in this age group, although often trees had multiple missing limbs, evidenced by stem scars. Other species which contributed to the canopy foliage of stands in this age group were *Beilschmiedia*, *Dysoxylum*, *Vitex* and *Kunzea*.

Table 5.1: Stem density (stems ha^{-1}) and relative stem density (%) for *Metrosideros excelsa* and associated species in forest age groups 0–60 years, 60–180 years, 180–300 years and >300 years. (d) = dead stems.

Age Group	0-60 years		60-180 years		180-300 years		300 + years	
	Density (stems ha^{-1})	Relative den. (%)	Density (stems ha^{-1})	Relative den. (%)	Density (stems ha^{-1})	Relative den. (%)	Density (stems ha^{-1})	Relative den. (%)
Beilschmiedia tawa	0	-	0	-	6.25 ± 17.7	0.1	25.0 ± 32.2	0.9
Brachyglottis repanda	131.3 ± 283	3.3	191.7 ± 227.1	4.0	428.1 ± 515.2	9.8	78.6 ± 86.0	3.0
Carmichaelia australis	0	-	0	-	3.1 ± 8.8	0.1	3.6 ± 9.5	0.1
Carpodetus serratus	0	0.0	3.1 ± 12.5	0.1	0	-	3.6 ± 9.5	0.1
Coprosma lucida	60.4 ± 135	1.7	456.7 ± 398.9	9.7	381.3 ± 638.0	8.8	82.1 ± 175.4	3.1
Coprosma grandifolia	0	-	3.1 ± 12.5	0.1	6.3 ± 11.6	0.1	14.3 ± 37.8	0.5
Coprosma macrocarpa	31.3 ± 64.9	0.9	345.3 ± 626.7	7.4	328.2 ± 537.8	7.4	10.7 ± 19.6	0.4
Coprosma repens	120.8 ± 418.5	3.0	169.6 ± 678.5	3.6	0	-	0	-
Coprosma robusta	368.8 ± 470.6	9.1	6.3 ± 19.4	0.1	43.8 ± 71.65	1.0	35.7 ± 53.8	1.3
Cordyline australis	35.4 ± 68.6	1.0	0	-	3.1 ± 8.8	0.1	0	-
Corynocarpus laevigatus	0	-	6.3 ± 19.4	0.1	6.3 ± 11.6	0.1	3.6 ± 9.5	0.1
Cyathea dealbata	66.7 ± 177.5	1.7	101.6 ± 142.1	2.2	140.6 ± 211.7	3.2	271.4 ± 220.5	10.2
Cyathea medullaris	27.1 ± 39.10	0.7	15.6 ± 44.6	0.3	50.0 ± 51.8	1.1	89.3 ± 122.4	3.4
Dicksonia squarrosa	0	-	1.6 ± 6.25	0.0	0	-	21.4 ± 56.7	0.8
Dysoxylum spectabile	0	-	5.2 ± 11.3	0.1	59.4 ± 92.5	1.4	146.0 ± 248.8	5.5
Entelea arborescens	25 ± 86.6	0.6	6.2 ± 25.0	0.1	0	-	0	-
Geniostoma rupestre	252.1 ± 379.0	6.1	353.0 ± 469.0	7.5	653.1 ± 823.9	15.0	107.1 ± 128.1	4.0
Knightia excelsa	14.6 ± 31.0	0.4	79.6 ± 163.6	1.7	50.0 ± 35.4	1.1	7.1 ± 18.9	0.3
Kunzea ericoides	105.8 ± 261.5	2.6	21.4 ± 48.5	0.5	53.1 ± 102.2	1.2	96.4 ± 131.0	3.6
Leptospermum scoparium	137.5 ± 376.0	3.3	0	-	0	-	0	-
Leptecophylla juniperina	0	-	6.25 ± 25.0	0.1	0	-	17.9 ± 47.2	0.7
Litsea calicaris	0	-	155.2 ± 396.7	3.3	187.5 ± 251.0	4.3	96.4 ± 212.9	3.6
Leucopogon fasciculatus	33.3 ± 65.1	0.9	37.5 ± 396.7	0.8	9.4 26.5	0.2	67.9 ± 138.2	2.6
Hedycarya aborea	22.9 ± 34.4	0.6	142.7 ± 187.5	3.0	384.4 ± 446.0	8.8	96.4 ± 122.0	3.6
Hebe stricta	25 ± 62.1	0.7	0	-	0	-	0	-
Macropiper excelsum	8.3 ± 16.2	0.2	239.1 ± 510.7	5.1	237.5 ± 367.4	5.5	432.1 ± 586.6	16.3
Melicytus ramiflorus	270.8 ± 532.5	6.6	217.2 ± 218.7	4.6	275.0 ± 215.5	6.3	189.3 ± 173.7	7.1
Melicytus novae-zelandiae	0	-	3.1 ± 12.5	0	0	-	0	-
Metrosideros excelsa	1120.8 ± 938.8	28.0	437.5 ± 275.7	9.3	225.0 ± 367.4	5.2	82.1 ± 140.5	3.1
Metrosideros excelsa (d)	152.1 ± 330.2	3.8	51.0 ± 87.8	1.1	15.6 ± 70.7	0.4	0	-
Myoporum laetum	4.2 ± 14.4	0.1	0	-	0	-	0	-
Myrsine autralis	212.5 ± 386.2	5.5	678.6 ± 1000.8	14.4	228.0 ± 183.1	5.1	92.9 ± 137.4	3.5
Nothofagus truncata	0	-	0	-	0	-	7.1 ± 18.9	0.3
Olearia rani	4.2 ± 14.4	0.1	17.7 ± 40.0	0.4	0	-	3.6 ± 9.5	0.1
Pittosporum crassifolium	0	-	95.3 ± 298.4	2.0	0	-	7.1 ± 18.9	0.3
Pittosporum umbellatum	0	-	0	-	9.4 ± 26.5	0.2	25.0 ± 66.1	0.9
Pittosporum tenuifolium	45.8 ± 94.6	1.1	31.8 ± 83.4	0.7	34.4 ± 58.2	0.8	10.7 ± 28.3	0.4
Pseudopanax arboreus	156.3 ± 36.5	3.8	80.7 ± 157.5	1.7	96.9 ± 144.5	2.2	42.9 ± 59.0	1.6
Pseudopanax crassifolius	4.2 ± 14.43	0.1	3.1 ± 12.5	0.1	3.1 ± 8.8	0.1	10.7 ± 18.9	0.4
Pseudopanax lessonii	193.7 ± 344.9	4.8	647.9 ± 1441.8	13.8	365.6 ± 904.6	8.4	192.9 ± 445.0	7.3
Weinmannia racemosa	12.5 ± 43.3	0.3	51.5 ± 173.8	1.1	28.1 ± 70.0	0.6	10.7 ± 28.3	0.4
Vitex lucens	39.6 ± 137.1	1.0	3.1 ± 8.5	0.1	6.3 ± 11.6	0.1	25.0 ± 47.2	0.9
others*	56.2 ± 77.5	1.4	17.7 ± 18.3	0.8	18.7 ± 10.7	1.1	10.7 ± 37.9	9.3
Total	4255 ± 1522	-	4875 ± 1606	-	4437 ± 1782	-	2564 ± 1779	-

**= Alectryon excelsus, Aristotelia serrata, Beilschmiedia tarairi, Coriaria arborea, Cotoneaster glaucophyllus, Crataegus monogyna, Dacrycarpus dacrydioides, Dodonaea viscosa, Freycinetia banksii, Ligustrum sinense, Melicytus novae-zelandiae, Metrosideros robusta, Nothofagus truncata, Pseudopanax hybrid, Racosperma mearnsii, Rhopalostylis sapida, Sophora microphylla, Ulex europaeus.*

Table 5.2: Basal area ($m^2\ ha^{-1}$) and relative basal area (%) for *Metrosideros excelsa* and associated species in forest age groups 0–60 years, 60–180 years, 180–300 years and >300 years. (d) = dead stems

Age Group	0-60 years		60-180 years		180-300 years		300 + years	
	Basal Area ($m^2\ ha^{-1}$)	Relative BA (%)	Basal Area ($m^2\ ha^{-1}$)	Relative BA (%)	Basal Area ($m^2\ ha^{-1}$)	Relative BA (%)	Basal Area ($m^2\ ha^{-1}$)	Relative BA (%)
Beilschmiedia tawa	0	-	0	-	0.01 ± 0.15	0.1	1.21 ± 2.27	1.5
Brachyglottis repanda	0.08 ± 0.20	0.2	0.19 ± 0.24	0.2	0.80 ± 1.26	0.9	0.17 ± 0.27	1.0
Carmichaelia australis	0	-	0	-	0.01 ± 0.02	0.0	0.01 ± 0.03	0.0
Carpodetus serratus	0	-	0.01 ± 0.03	0.0	0	-	0.01 ± 0.04	0.0
Coprosma lucida	0.05 ± 0.12	0.1	0.63 ± 0.71	0.8	0.60 ± 0.97	0.6	0.10 ± 0.22	0.5
Coprosma grandifolia	0	-	0	-	0.01 ± 0.04	-	0.02 ± 0.05	0.0
Coprosma macrocarpa	0.12 ± 0.35	0.3	0.32 ± 0.58	0.4	0.39 ± 0.04	0.4	0.10 ± 0.05	0.5
Coprosma repens	0.06 ± 0.22	0.2	0.37 ± 1.47	0.5	0	-	0	-
Coprosma robusta	0.42 ± 0.42	1.1	0.02 ± 0.56	0.0	0.15 ± 0.29	0.2	0.13 ± 0.26	0.2
Coriaria arborea	0.92 ± 2.17	2.4	0	-	0	-	0	-
Cordyline australis	0.37 ± 0.75	1.0	0	-	0.14 ± 0.40	0.2	0	-
Corynocarpus laevigatus	0	-	0.13 ± 0.49	0.2	0.01 ± 0.02	0.0	0.01 ± 0.01	0.0
Cyathea dealbata	2.45 ± 7.15	6.0	3.07 ± 4.19	4.1	4.20 ± 6.29	4.5	6.48 ± 4.66	7.6
Cyathea medullaris	0.71 ± 1.35	1.9	0.39 ± 1.36	0.5	0.76 ± 0.80	0.8	2.44 ± 3.66	1.0
Dicksonia squarrosa	0	-	0.02 ± 0.08	0.0	0	0.0	0.23 ± 0.61	0.1
Dysoxylum spectabile	0	-	0.01 ± 0.02	0.0	0.08 ± 0.14	0.1	2.47 ± 5.01	3.1
Entelea arborescens	0.30 ± 1.14	0.8	0.01 ± 0.04	0.0	0	-	0	-
Geniostoma rupestre	0.33 ± 0.66	0.9	0.42 ± 0.60	0.6	0.67 ± 0.91	0.7	0.14 ± 0.17	0.2
Knightia excelsa	0.23 ± 0.48	0.6	6.09 ± 9.40	8.1	3.22 ± 3.61	3.4	0.08 ± 0.01	0.0
Kunzea ericoides	0.45 ± 0.80	1.2	0.76 ± 2.12	1.0	1.85 ± 4.23	2.0	3.74 ± 4.89	4.5
Leptospermum scoparium	0.18 ± 0.45	0.5	0	-	0	-	0	-
Leptecophylla juniperina	0	-	0.01 ± 0.02	0.0	0	-	0.03 ± 0.08	-
Litsea calicaris	0	-	0.21 ± 0.37	0.3	0.55 ± 0.69	0.6	1.49 ± 4.89	1.7
Leucopogon fasciculatus	0.05 ± 0.10	0.1	0.08 ± 0.14	0.1	0.02 ± 0.07	0.0	0.14 ± 4.89	0.0
Hedycarya aborea	0.03 ± 0.05	0.1	0.39 ± 0.63	0.5	0.64 ± 0.82	0.7	1.73 ± 4.89	2.1
Hebe stricta	0.01 ± 0.02	0.0	0	-	0	-	0	-
Macropiper excelsum	0.01 ± 0.01	0.0	0.34 ± 0.91	0.5	0.30 ± 0.57	0.3	0.26 ± 4.89	0.4
Melicytus ramiflorus	1.03 ± 2.9	2.7	0.72 ± 0.62	1.0	0.90 ± 0.69	1.0	1.56 ± 4.89	1.8
Melicytus novae-zelandiae	0	-	0.01 ± 0.01	0.1	0	-	0	-
Metrosideros excelsa	26.6 ± 16.97	70.4	52.98 ± 26.72	70.6	72.87 ± 40.30	77.8	53.49 ± 4.89	63.4
Metrosideros excelsa (d)	0.71 ± 1.81	1.5	0.91 ± 1.16	1.0	0.63 ± 1.54	0.7	0	-
Myoporum laetum	0.10 ± 0.39	0.3	0	-	0	-	0	-
Myrsine autralis	0.71 ± 1.65	1.9	1.86 ± 2.68	2.5	0.72 ± 0.500	0.8	0.23 ± 0.50	0.3
Olearia rani	0.09 ± 0.35	0.2	0.04 ± 0.10	0.1	0	-	0.01 ± 0.02	-
Pittosporum crassifolium	0.03 ± 0.10	0.1	0.03 ± 0.12	0.0	0	-	0.02 ± 0.03	-
Pittosporum umbellatum	0	-	0	-	0.04 ± 0.13	0	0.24 ± 0.64	0.1
Pittosporum tenuifolium	0.15 ± 0.31	0.4	0.08 ± 0.22	0.1	0.31 ± 0.50	0.3	0.10 ± 0.27	0.4
Pseudopanax arboreus	0.41 ± 1.21	1.1	0.42 ± 1.53	0.6	0.56 ± 0.84	0.3	0.21 ± 0.27	0.7
Pseudopanax crassifolius	0	-	0.29 ± 0.94	0.4	0.01 ± 0.04	0.1	0.11 ± 0.29	0.1
Pseudopanax lessonii	0.47 ± 1.02	1.2	3.34 ± 6.91	4.4	2.93 ± 7.95	3.1	1.02 ± 1.86	1.2
Weinmannia racemosa	0.41 ± 1.14	1.1	1.76 ± 6.40	2.3	0.72 ± 1.59	0.8	1.08 ± 0.89	1.3
Vitex lucens	0.80 ± 3.00	2.1	0.01 0.01	0.0	0.14 ± 0.36	0.1	3.41 ± 7.00	4.4
Others*	0.09 ± 3.01	0.7	0.10 ± 5.00	0.9	0.07 ± 0.68	0.1	1.00 ± 3.01	0.9
Total	48.3 ± 24.0	-	76.4 ± 23.4	-	95.0 ± 35.0	-	85.3 ± 34.3	-

**= Alectryon excelsus, Aristotelia serrata, Beilschmiedia tarairi, Coriaria arborea, Cotoneaster glaucophyllus, Crataegus monogyna, Dacrycarpus dacrydioides, Dodonaea viscosa, Freycinetia banksii, Ligustrum sinense, Melicytus novae-zelandiae, Metrosideros robusta, Nothofagus truncata, Pseudopanax hybrid, Racosperma mearnsii, Rhopalostylis sapida, Sophora microphylla, Ulex europaeus.*

5.4.3 Species distribution with forest age

A number of species were common in all four age groups; and thus the distribution of these species within *Metrosideros* forest is unrelated to forest age. Common and widely distributed species contributed largely to the overall forest composition of each age group, therefore examining the floristic composition alone will not reveal the more subtle developmental trends. The following section reports on the variation in species density and basal area across the forest age groups.

Early colonist species

Metrosideros had the highest stem density in 0–60 year old quadrats (1120.8 stems ha^{-1}), and this then decreased across the age groupings due to self -thinning. The rate of stem loss was highest between the 0–60 and 60–180 year old stands (annual loss of c. 11 stems ha^{-1}) and showed a steady decrease thereafter (annual loss of c. 1.75 stems ha^{-1}). Standing dead stems of *Metrosideros* showed this same pattern across groups, however at much lower densities (0–152.1 stems ha^{-1}). The basal area of live *Metrosideros* stems in the 0–60 year age group was 26.6 $m^2 ha^{-1}$, and this increased with increasing age, peaking in the 180–300 year old quadrat stands (72.87 m^2 ha^{-1}). The basal area of dead *Metrosideros* stems initially increased from 0.71 m^2 ha^{-1} in the 0–60 year old group to 0.91 m^2 ha^{-1} in the 60–180 year old group; where it was at its maximum (Figure 5.2a).

Cordyline was also an early successional/colonist species, present in the canopy amongst young *Metrosideros* forest on Moutohora and in Matata Scenic Reserve. Similar to *Metrosideros*, the density of *Cordyline* was highest in the 0–60 year old quadrat group (35.4 stems ha^{-1}); this then rapidly decreased, with the species only present at insignificant rates in one of the older age groups (180–300 years). The basal area of *Cordyline* showed the same trend across the quadrat age groupings, ranging from 37.0–0.14 $m^2 ha^{-1}$. *Kunzea* was also an early colonist, establishing with *Metrosideros* and also appeared to lose stems to self-thinning. No other species of significance reached their highest densities in the 0–60 year old stands.

Early and mid successional species

The majority of species present in the youngest age group (0–60 years) increased in both density and basal area across age groups e.g. *P. crassifolius*, *C. lucida* and *K. excelsa*. A suite of species also appeared in the 60–180 year age group which

were not present in the younger stands; such species included *Litsea*, *Dysoxylum*, *Corynocarpus*, *D. squarossa* and *P. crassifolius*. The species *Corynocarpus*, *Knightia*, *P. lessonii* and *C. lucida* generally peaked in both density and basal area in the 60–180 year old age group, decreasing thereafter. Conversely the densities of *Litsea* and *Hedycarya* continued to increase through the 60–180 year group, peaking in the 180–300 year old age group and thus are prominent in mid-late *Metrosideros* forest successions. *Dysoxylum* also increased in both basal area and density with increasing group age and reached a maximum density and basal area (146 stems ha^{-1} and 2.47 m^2 ha^{-1} respectively) in stands >300 years old.

Late successional species

A suite of species appeared in the 180–300 and >300 year old age groups that were not present in the younger two age groupings. Species included *Beilschmiedia*, *Carmichaelia australis* and *Pittosporum umbellatum* (Table 5.5); the latter two species were only present at low densities. The density of *Beilschmiedia* increased from 6.25 stems ha^{-1} in the 80–300 age group, to 25.0 stems ha^{-1} in the ≥300 year age group. The basal area of *Beilschmiedia* showed the same trend, increasing from 0.01 to 1.21 m^2 ha^{-1}. Species *Alectryon*, *Nothofagus* and *Rhopalostylis sapida*, not individually shown on Table 5.1 and Table 5.2, due to their low densities, were also only present in the ≥300 year old age group.

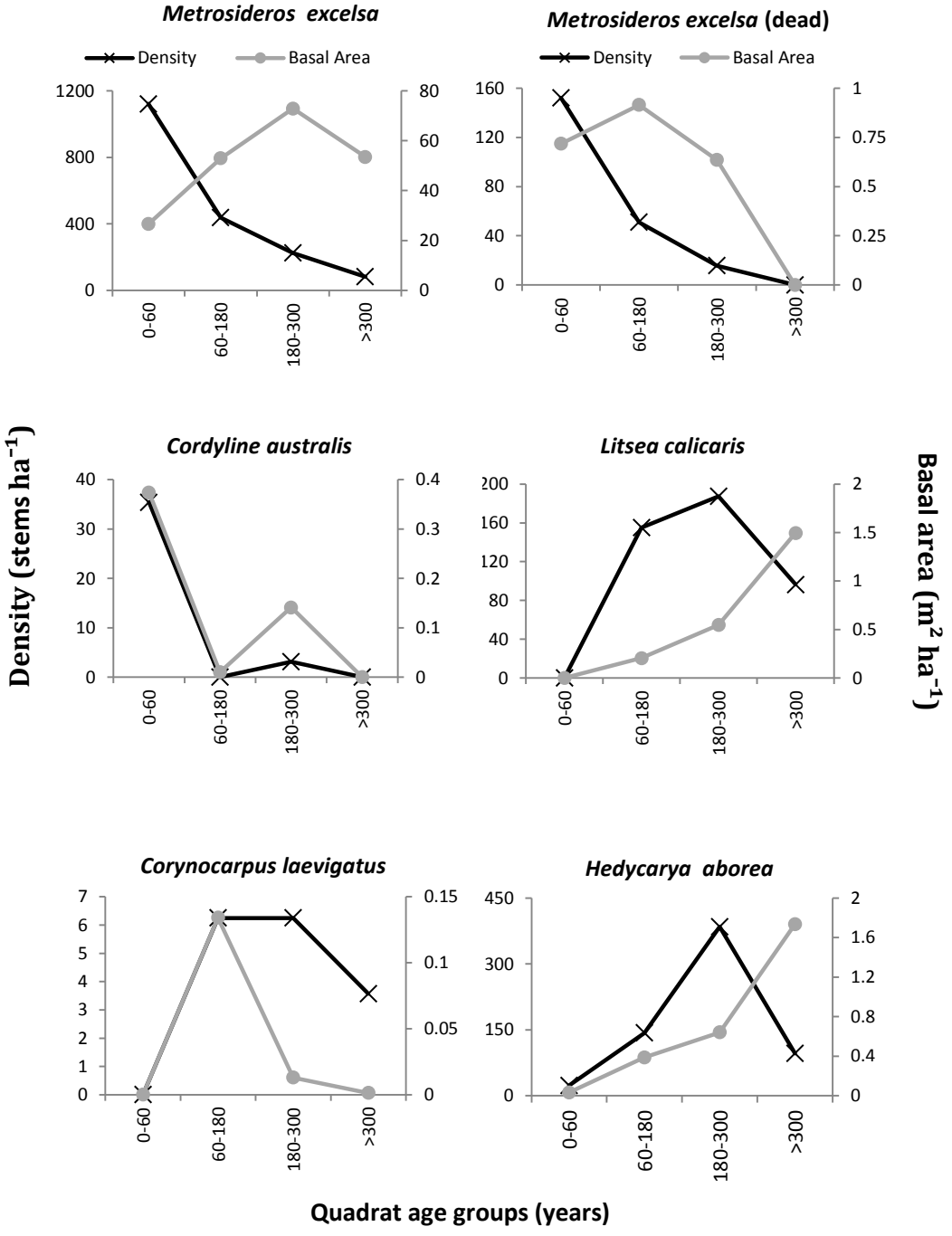


Figure 5.2A: Average density and Basal area of common species in *Metrosideros excelsa* forest in four forest age groups; 0–60 years, 60–180 years, 180–300 years and >300 years.

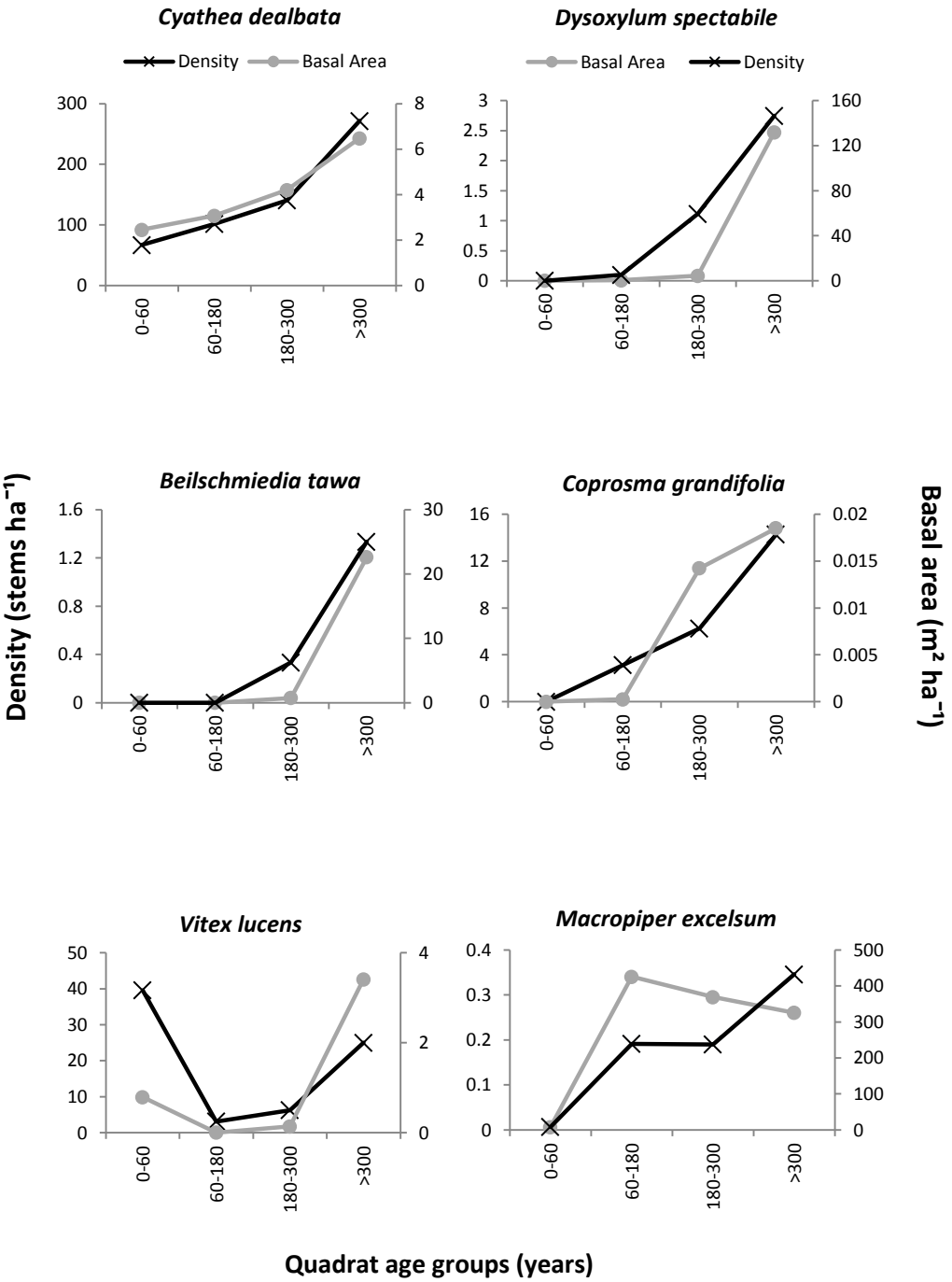


Figure 5.3B: Average density and Basal area of common species in *Metrosideros excelsa* forest in four forest age groups; 0–60 years, 60–180 years, 180–300 years and >300 years.

5.4.4 Seedling and sapling occurrence and distribution

The differential interspecific growth and survival of seedlings and saplings (collectively referred to here as juveniles) in the forest understory, causes changes in species composition during succession (Delucia et al. 1998). Consequently the differential occurrence of species juveniles, during *Metrosideros* forest development is indicative of the forests successional trajectory. *Metrosideros* and associated species seedling and sapling densities are presented here, along with a standard deviation as a measure of variance, for each of the four forest age groups (Table 5.3 and Table 5.4).

Juveniles of *Metrosideros*, *Kunzea*, *H. stricta* and *Coriaria arborea* were common in the 0–60 your old stands, these species colonised bare substrates on Awataraiki Stream terrace, and had formed dense scrubby thickets within six years of the disturbance. Juveniles of *Geniostoma*, *C. robusta*, *M. excelsum*, *P. lessonii* and *P. arboreus* were also common in the 0–60 year old stands; however were generally found in young forest as opposed to scrub. *Phyllocladus trichomanoides* juveniles were common in Opape quadrats (0–60 years old), however were found predominantly as seedlings and not saplings. This may suggest that either *P. trichomanoides* seedlings are able to establish but unable to persist, or that the arrival of this *P. trichomanoides* seedlings is recent and the species will persist and later become a prominent component of the vegetation.

Litsea, *M. australis* and *Hedycarya* juveniles became increasingly common in the 60–180 and 180–300 year old stands, however were present in comparably low densities in stands >300 years old. Consequently, the regeneration of these species in mature *Metrosideros* forest is less prolific than that in developing forest and are instead displaced by later successional species. The increasing densities of *Dysoxylum*, *Vitex*, *Corynocarpus* and *Beilschmiedia* juveniles the 180–300 and >300 year groups is indicative of the species future dominance and subsequent replacement of *Metrosideros* in the canopy of mature forest.

Table 5.3: Seedling density (stems ha^{-1}) for *Metrosideros excelsa* and associated species, across forest age groups 0–60 years, 60–180 years, 180–300 years and >300 years.

Species	0-60 years		60-180 years		180-300 years		>300 years	
	Density (stems ha^{-1})	Relative *d* (%)	Density (stems ha^{-1})	Relative d (%)	Density (stems ha^{-1})	Relative d (%)	Density (stems ha^{-1})	Relative d (%)
Alectryon excelsus	17 ± 14	0.2	8 ± 6	0.1	-	-	-	-
Beilschmiedia tawa	17 ± 9	0.2	58 ± 20	0.5	100 ± 31	1.6	143 ± 45	1.8
Brachyglottis repanda	100 ± 62	0.9	408 ± 102	4.2	280 ± 96	4.6	129 ± 49	1.6
Carpodetus serratus	-	-	-	-	360 ± 201	5.9	29 ± 19	0.4
Coprosma grandifolia	17 ± 14	0.2	25 ± 19	0.3	-	-	43 ± 28	0.5
Coprosma lucida	108 ± 37	1.0	1150 ± 619	11.7	180 ± 62	3.0	557 ± 268	6.9
Coprosma macrocarpa	167 ± 93	1.5	-	-	-	-	-	-
Coprosma rhamnoides	375 ± 297	3.4	75 ± 56	-	-	-	-	-
Coprosma robusta	317 ± 94	2.9	33 ± 19	0.3	200 ± 98	3.3	-	-
Cordyline australis	16 ± 14	0.2	-	-	-	-	-	-
Coriaria arborea	400 ± 229	3.7	-	-	-	-	-	-
Corynocarpus laevigatus	-	-	75 ± 50	0.8	160 ± 89	2.6	329 ± 135	4.1
Cyathea dealbata	-	-	8 ± 6	0.1	-	-	129 ± 35	1.6
Dysoxylum spectabile	-	-	42 ± 17	0.4	520 ± 198	8.6	271 ± 101	3.4
Geniostoma rupestre	1700 ± 385	15.5	2842 ± 858	29.0	860 ± 293	14.1	942 ± 174	11.7
Hebe stricta	258 ± 143	2.4	-	-	180 ± 101	3.0	-	-
Hedycarya aborea	158 ± 60	1.4	1541 ± 619	15.7	280 ± 74	4.6	814 ± 193	10.1
Helichrysum lanceolatum	150 ± 85	1.4	41 ± 31	0.4	-	-	-	-
Knightia excelsa	33 ± 19	0.3	158 ± 60	1.6	60 ± 34	1.0	57 ± 24	0.7
Kunzea ericoides	3383 ± 1895	30.9	16 ± 13	0.2	-	-	-	-
Leptospermum scoparium	16 ± 14	0.2	-	-	-	-	-	-
Leucopogon fasciculatus	91 ± 27	0.8	191 ± 115	2.0	220 ± 123	3.6	-	-
Litsea calicaris	-	0.0	1325 ± 632	13.5	400 ± 85	6.6	400 ± 166	5.0
Macropiper excelsum	383 ± 214	3.5	516 ± 222	5.3	640 ± 65	10.5	557 ± 136	6.9
Melicytus micranthus	-	0.0	33 ± 19	0.3	100 ± 56	1.6	-	-
Melicytus ramiflorus	292 ± 109	2.7	183 ± 19	1.9	120 ± 54	2.0	328 ± 67	4.1
Metrosideros excelsa	2217 ± 1283	20.2	-	-	160 ± 65	2.6	-	-
Myrsine autralis	92 ± 63	0.8	441 ± 170	4.5	260 ± 72	4.3	486 ± 158	6.0
Olearia rani	8 ± 7	0.1	-	-	-	2.9	86 ± 57	1.1
Phyllocladus trichomanoides	100 ± 57	0.9	-	-	-	-	-	-
Pittosporum crassifolium	67 ± 55	0.6	-	-	-	-	-	-
Pittosporum tenuifolium	-	-	8 ± 6	0.1	40 ± 22	0.7	14 ± 9	0.2
Pittosporum umbellatum	-	-	-	-	240 ± 134	3.9	29 ± 19	0.4
Pseudopanax arboreus	142 ± 63	1.3	166 ± 64	1.7	240 ± 52	3.9	100 ± 43	1.2
Pseudopanax lessonii	17 ± 9	0.2	308 ± 212	3.1	40 ± 22	0.7	171 ± 61	2.1
Rhopalostylis sapida	-	-	75	0.8	120 ± 54	2.0	357 ± 155	4.4
Ripogonum scandens	-	-	25	0.3	40 ± 14	0.7	-	-
Schefflera digitata	-	-	25	0.3	-	-	29 ± 19	0.4
Vitex lucens	17 ± 14	0.2	-	-	100 ± 56	1.6	29 ± 19	0.4
Weinmannia racemosa	33 ± 19	0.3	-	-	-	-	-	-
Others*	208	1.9	90	0.9	280	4.5	2027	25.1

**= Beilschmiedia tarairi, Coprosma lucida, Coprosma spathulata, Cotoneaster glaucophyllus, Cyathea cunninghamii, Dicksonia squarrosa, Freycinetia banksii, Leptecophylla juniperina, Ligustrum sinense, Melicope ternata, Olearia albida, Olearia pachyphylla, Pittosporum umbellatum, Sophora microphylla.*

Table 5.4: Sapling density (stems ha^{-1}) for *Metrosideros excelsa* and associated species, across forest age groups 0–60 years, 60–180 years, 180–300 years and >300 years.

Species	0-60 years		60-180 years		180-300 years		>300 years	
	Density (stems ha^{-1})	Relative d (%)	Density (stems ha^{-1})	Relative d (%)	Density (stems ha^{-1})	Relative d (%)	Density (stems ha^{-1})	Relative d (%)
Alectryon excelsus	8 ± 7	0.2	-	-	-	-	-	-
Beilschmiedia tawa	-	-	19 ± 16	0.3	29 ± 12	0.4	86 ± 47	2.3
Brachyglottis repanda	275 ± 192	5.8	185 ± 70	3.0	382 ± 134	4.9	114 ± 54	3.1
Coprosma grandifolia	8 ± 7	0.2	4 ± 5	0.1	18 ± 9	0.2	43 ± 28	1.2
Coprosma lucida	100 ± 37	2.1	828 ± 528	12.3	418 ± 185	5.3	71 ± 31	1.9
Coprosma macrocarpa	133 ± 80	2.8	590 ± 207	8.8	273 ± 78	3.5	-	-
Coprosma rhamnoides	141 ± 4.60	3.0	4 ± 5	0.1	-	-	-	-
Coprosma robusta	416± 5.97	8.8	-	-	218 ± 113	2.8	-	-
Coriaria arborea	133 ± 100	2.8	-	-	-	-	-	-
Cordyline australis	33 ± 22	0.7	-	-	-	-	-	-
Cortaderia jubata	416 ± 244	8.8	-	-	-	-	-	-
Corynocarpus laevigatus	-	-	14 ±12	0.2	18 ± 9	0.2	29 ± 12	0.8
Cyathea dealbata	75 ± 44	1.6	47 ± 43	0.7	55 ± 20	0.7	357 ± 95	9.7
Dysoxylum spectabile	-	-	23 ± 13	0.4	73 ± 24	0.9	43 ± 20	1.9
Geniostoma rupestre	1066 ± 217	22.5	1352 ± 721	20.2	1055 ± 166	13.4	400 ± 103	10.8
Hebe stricta	225 ± 111	4.7	23 ± 27	0.4	-	-	100 ± 56	2.7
Hedycarya aborea	58 ± 38	1.2	185 ± 73	2.8	418 ± 62	5.3	186 ± 49	5.0
Helichrysum lanceolatum	16 ± 15	0.4	4 ± 5	0.1	-	-	-	-
Knightia excelsa	-	-	42 ± 38	0.6	-	-	57 ± 37	1.5
Kunzea ericoides	216 ± 129	4.6	19 ±21	0.3	-	-	71 ± 47	1.9
Leptospermum scoparium	108 ± 62	2.3	-	-	-	-	-	-
Litsea calicaris	8± 7	0.2	1071 ± 603	16.0	1055 ± 255	13.4	386 ± 105	10.4
Leucopogon fasciculatus	100 ± 45	2.1	66 ± 54	1.0	-	-	-	-
Macropiper excelsum	208 ± 142	4.4	676 ± 206	10.1	1836 ± 377	23.4	200 ± 76	5.4
Melicytus micranthus	-	-	4 ± 5	0.1	-	-	-	-
Melicytus ramiflorus	275 ± 148	5.8	80 ±50	1.2	309 ± 97	3.9	343 ± 85	9.3
Metrosideros excelsa	50 ± 31	1.1	10 ± 11	0.1	-	-	-	-
Myrsine autralis	108 ± 66	2.3	943 ± 233	14.1	1018 ± 176	13.0	100 ± 66	2.7
Olearia rani	8 ±7	0.2	-	-	55 ± 28	0.7	14 ± 9	0.4
Pittosporum crassifolium	8 ± 7	0.2	43 ± 38	0.6	-	-	29 ± 19	0.8
Pittosporum tenuifolium	-	-	5 ± 5	0.1	-	-	14 ± 9	0.4
Pseudopanax arboreus	208 ± 111	4.4	186 ± 48	2.8	381 ± 113	4.9	43 ± 20	1.2
Pseudopanax lessonii	116 ± 47	2.5	71 ± 48	1.1	73 ± 28	0.9	100 ± 35	2.7
Rhopalostylis sapida	-	-	43± 48	0.6	-	-	186 ± 77	5.0
Ripogonum scandens	-	-	5 ± 5	0.1	-	-	143 ± 84	3.9
Vitex lucens	-	-	10 ± 6	0.1	36 ± 12	0.5	14 ± 9	0.4
Others*	221	5.5	147	2.5	127	2.3	442	10.7

**= Beilschmiedia tarairi, Coprosma arborea, Coprosma lucida, Coprosma spathulata, Coprosma repens, Cotoneaster glaucophyllus, Cyathea cunninghamii, Cyathea medullaris, Dicksonia squarrosa, Entelea arborescens, Freycinetia banksii, Leptecophylla juniperina, Ligustrum sinense, Melicope ternata, Olearia albida, Olearia pachyphylla, Pittosporum umbellatum, Prumnopitys ferruginea, Schefflera digitata, Sophora microphylla, Weinmannia racemosa.*

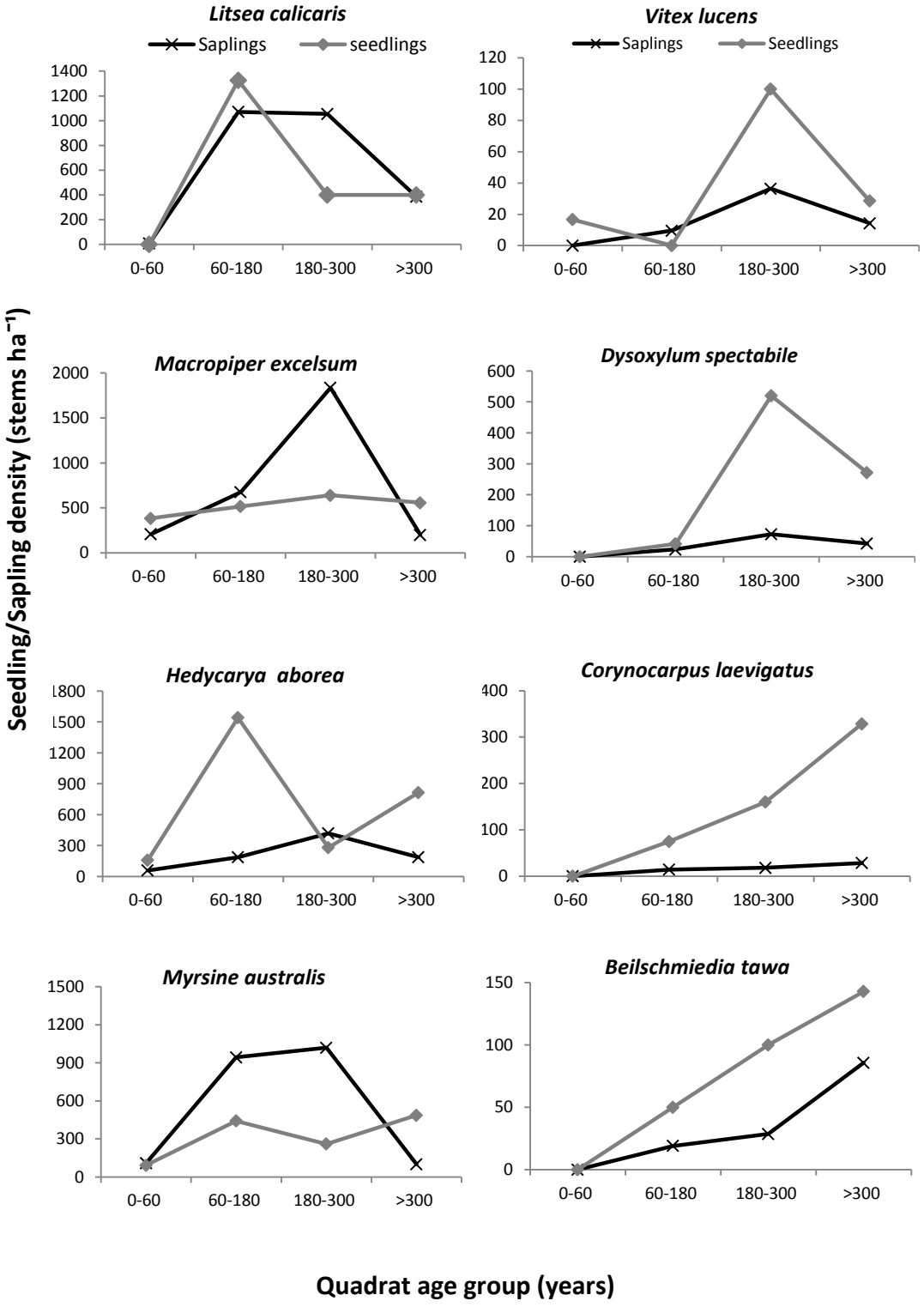


Figure 5.4: Average density of common seedling and sapling species in *Metrosideros excelsa* forest across the four forest age groups; 0–60 years, 60–180 years, 180–300 years and >300 years.

5.4.5 Diameter frequency distributions

The objectives of this study not only included the quantitative comparison of species composition across a spectrum of forest ages, but also the comparison of regenerative processes, which will allow developmental trajectories to be inferred. Stand structure, or the frequency distribution of differentially sized stems reflects previous establishment events. Stand structure is examined here for *Metrosideros* and key species.

The diameter frequency distribution of *Metrosideros* (Figure 5.5) is consistent with catastrophic or gap-phase regeneration. The structure of stems differs substantially between the four stand age groups. *Metrosideros* structure in the 0–60 year old stands consisted of many small stems, with the majority of stems between 10–20 cm dbh. The prevalence of dead stems within the 2–10 and 10–20 cm diameter classes suggests stands at this stage of development are fully stocked and undergoing a large degree of self-thinning. The frequency of *Metrosideros* stems decreased in the larger diameter size classes, and with the exception of seedlings and saplings (present only at one locality), had a cohort structure. This is typical for a species whose regeneration strategy is tuned in to disturbance events and fails to regenerate beneath a closed canopy.

The structure of *Metrosideros* stems in the 60–180 and 180–300 year old stands consists of a cohort, with a modal size class of 30–40 and 40–50 cm dbh respectively. The lack seedlings and saplings indicates no recruitment of *Metrosideros* occurs after the initial colonisation event. The presence of a single large stem (162 cm dbh) in the in the 60–180 year old stands suggests this stem is a relic of a prior colonisation episode. The diameter frequency distribution of stems in the >300 year was sporadic, with no stems <60 cm dbh present. The modal size class was 110–120 cm, however stems as large as 240 cm dbh were present; such trees are likely to exceed 1000 years. Quadrats located on steep sites such as coastal cliffs had larger variations in *Metrosideros* stem diameters, which is a likely result of numerous small scale disturbances, giving rise to a multi-modal population structures.

The diameter size class distribution of *Kunzea* indicates catastrophic and/or gap phase regeneration (Figure 5.6). Similarly to *Metrosideros*, the diameter frequency distribution of *Kunzea* also produced a reverse-J curve in the 0–60 year

old stands. High numbers of seedlings and saplings were present (>300 stems ha^{-1}), particularly in the scrub dominated sites. *Kunzea* stems in the 60–180 and 180–300 year old stands generally had a uni-modal distribution, with a high frequency of stems in the 2–5 cm diameter classes. This suggests there may be some recruitment of *Kunzea* occurring, possibly associated with canopy gaps. No seedlings or saplings were present in the 180–300 and >300 year old stands, and this suggests recruitment of *Kunzea* juveniles has ceased by this stage of forest development. The symmetrical size class distribution of *Kunzea* stems in the >300 year stands is a typical pattern of a species that establishes in large openings, as a cohort population.

A non-disturbed canopy structure was generally observed in *Metrosideros* forest >60 years old, thus the abundance of species in the understory reflects their shade tolerance. *Litsea* stems were only present as seedlings in stands less than 60 years old, thus indicating this species has a mid-successional status in forest succession. The diameter frequency distribution of *Litsea* is similar in the older three age groups; having a high frequency of saplings and seedlings compared to the larger diameter size classes (Figure 5.7). This is particularly evident in the 60–180 years old stands, were the frequency of seedlings and saplings reached their maximum of 1375 and 1071 stems ha^{-1}, respectively. The maximum diameter class occupied by *Litsea* stems increased with increasing group age; thus indicating that stems established between 60–180 years of forest development are persisting. The strongly skewed population structure of *Litsea* in the mid successional stands suggests a recent establishment.

The diameter frequency distributions of *Knightia* did not have a coherent pattern across age groups. Few stems were present in stands <60 years old, and these were of a small diameter size (<30 cm dbh).The structure of stems in the older three age groups illustrated reverse-J curves with sufficient seedling and sapling numbers to indicate regenerating populations. The structure of *P. lessonii* stems also generally followed a reverse-J curve, with the exception of those in the 180–300 year old stands which had a cohort structure (Figure 5.7). *Pseudopanax lessonii* was a common component of the forest understory in stands between 60–300 years old. The initial recruitment of *P. lessonii* stems appeared to occur between 60–180 years of forest development, when the density of juveniles peaked.

Beilschmiedia stems were only present as seedlings in stands <60 years old. The structure of *Beilschmiedia* stems show a reverse-J curve, indicating the species is capable of continuous regeneration beneath a closed canopy (Figure 5.8). The frequency and average size of *Beilschmiedia* stems increased with stand age; accordingly this suggests that stems established between 60–180 years of forest development are persisting, and increasing in abundance as forests mature. Similarly the frequency and average size of *Dysoxylum* stems also increased as stand age increased and the species diameter frequency distributions produced reverse-J curves in all forest age groups. Thus it is also likely *Dysoxylum* will continue to gain canopy dominance, particularly in stands immediately adjacent to the coast, where the species is more common than *Beilschmiedia*.

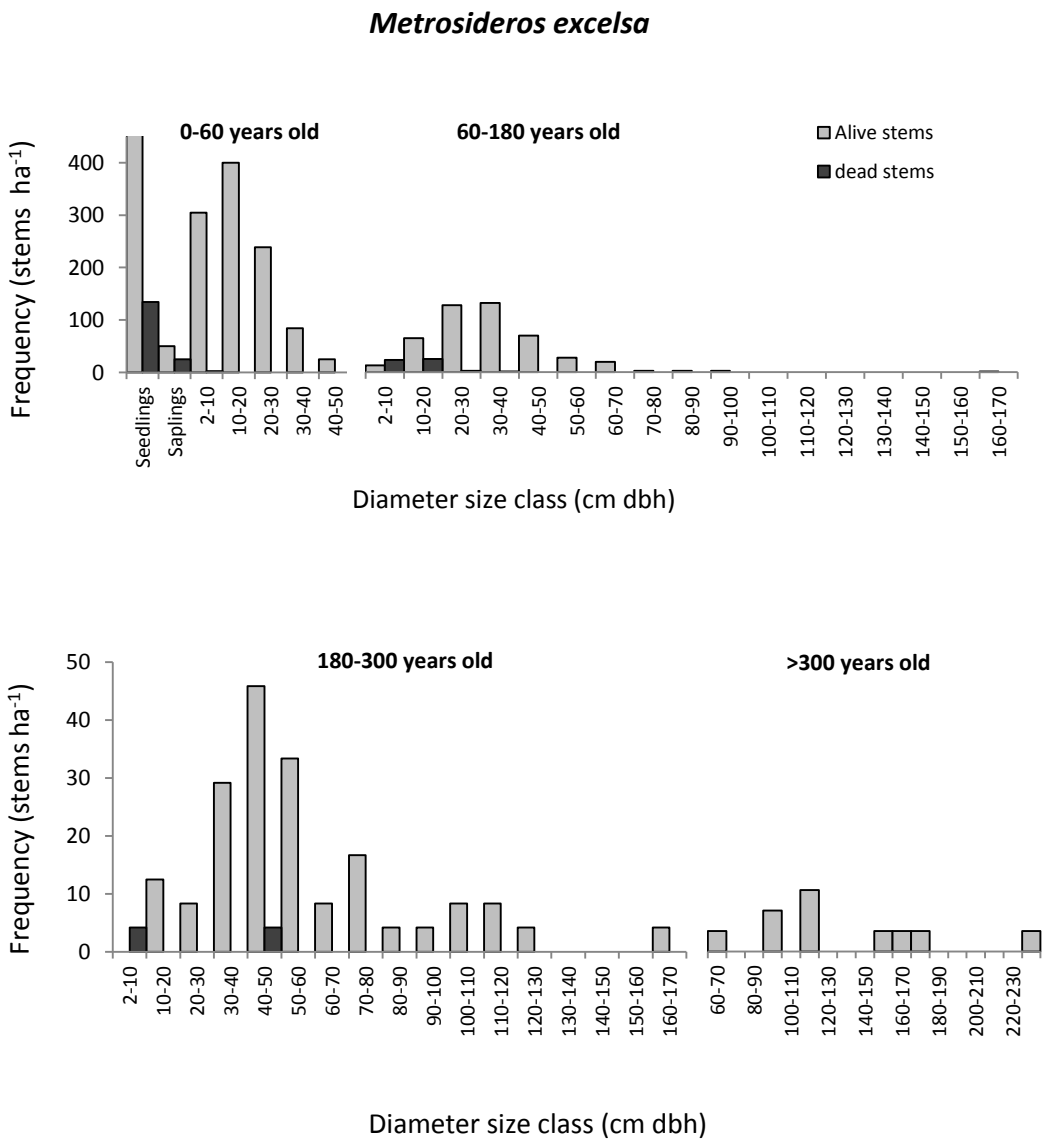
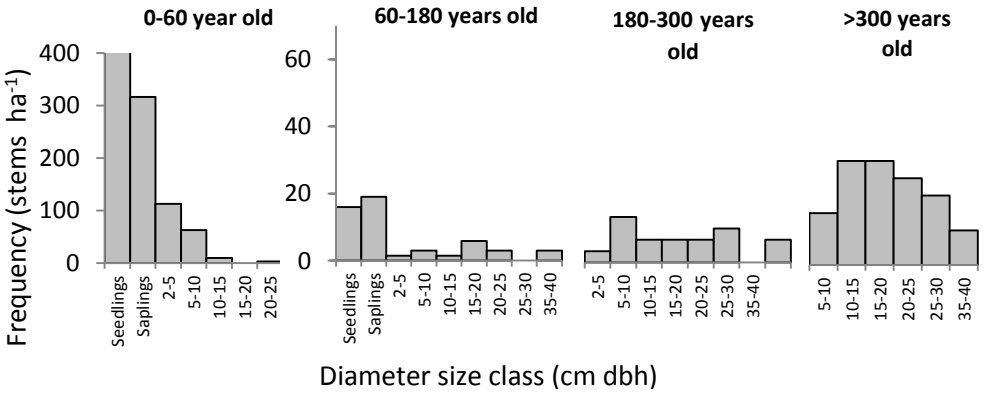
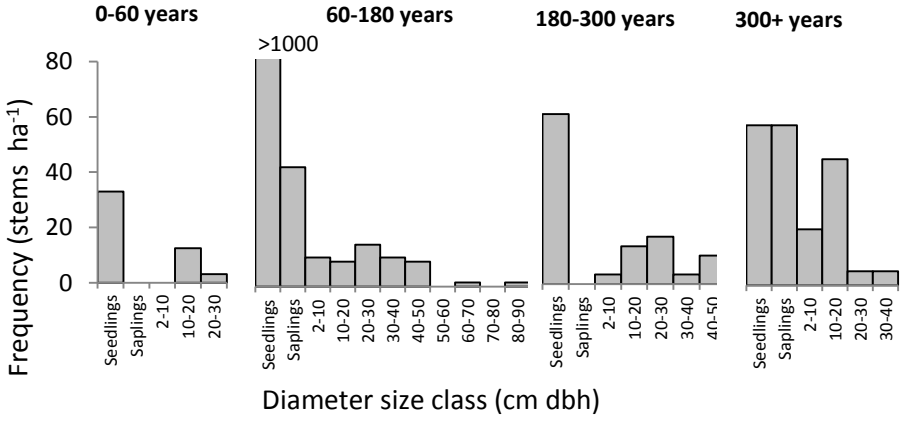


Figure 5.5: Percentage frequency distributions in diameter size classes of *Metrosideros excelsa* in four stand age groups; 0–60 years, 60–180 years, 180–300 years and >300 years. Seedlings are <50 cm tall. Saplings are >50 cm tall and less than 2 cm dbh.

Kunzea ericoides



Knightia excelsa



Pseudopanax lessonii

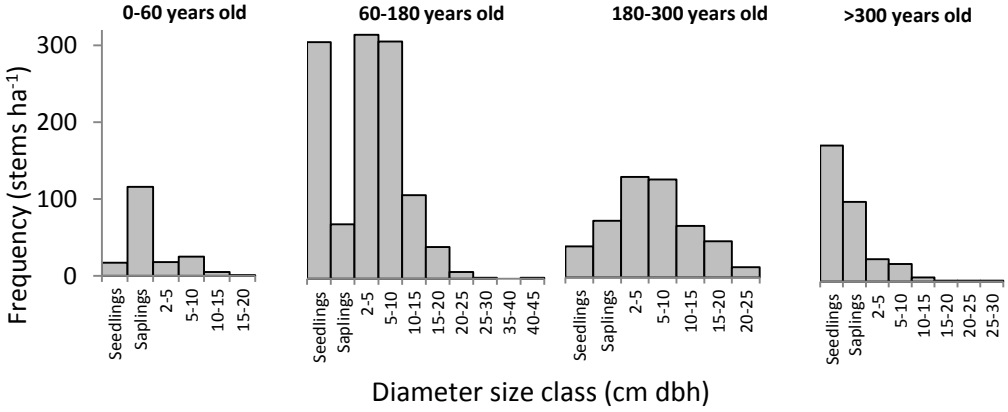


Figure 5.6: Percentage frequency distributions in diameter size classes of *Kunzea ericoides*, *Knightia excelsa* and *Pseudopanax lessonii* in four stand age groups; 0–60 years, 60–180 years, 180–300 years and >300 years. Seedlings are <50 cm tall. Saplings are >50 cm tall and less than 2 cm dbh.

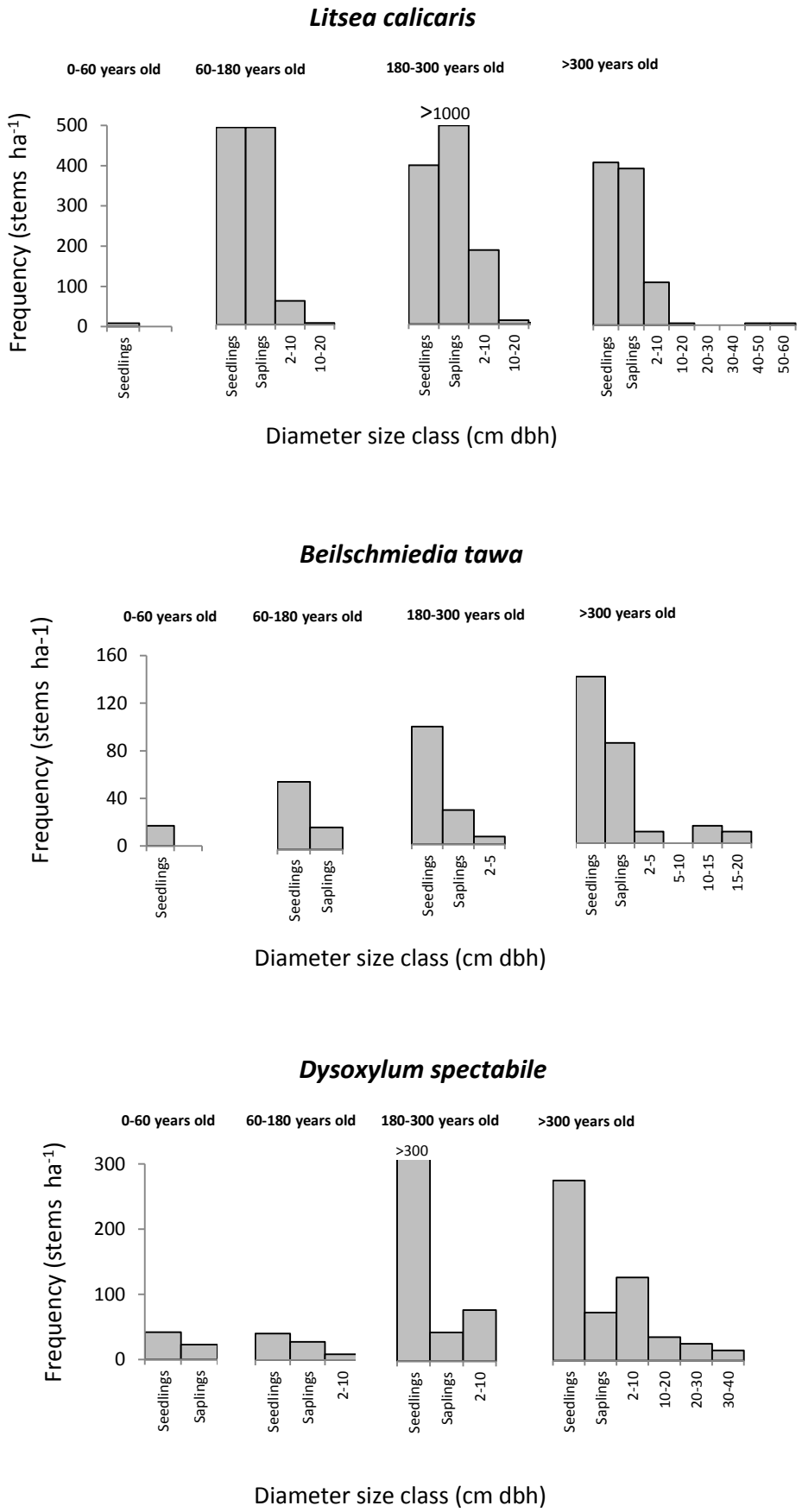


Figure 5.8: Percentage frequency distributions in diameter size classes of *Litsea calicaris*, *Beilschmiedia tawa*, and *Dysoxylum spectabile* in four stand age groups; 0–60 years, 60–180 years, 180–300 years and >300 years. Seedlings are <50 cm tall. Saplings are >50 cm tall and less than 2 cm dbh.

5.4.6 Re-measurement of permanent quadrats

Four permanent quadrats were re-measured; three quadrats on Tuhua and one quadrat on Motuotau, capturing 18 and 21 years of forest development, respectively. Permanent quadrat data were included in all prior analysis, however developmental trends are specifically analysed here. Tuhua quadrats were located at Panui Peninsula, Tikitikinahoa, and South East Bay; the Panui Peninsula and Tikitikinahoa quadrats were, in the previous analysis, grouped with the 60–180 year old stands, whereas the quadrat near South East Bay was considerably older, and grouped with the 180–300 year old quadrats. The permanent quadrat on Motuotau fell into two consecutive age groups; the data from the initial quadrat survey in 1990 was grouped with the 0–60 year old stands, whereas the 2011 re-measurement was included in the 60–180 year old group. Ages are consistent with the islands disturbance histories.

Total density of live stems generally increased in quadrats between the initial measurement and re-measurement; with the exception of the Motuotau quadrat, which had an overall decrease of 1131 stems ha^{-1}. This decrease in density was coupled with a large gain in total basal area of 49.1 $m^2 ha^{-1}$. The Tuhua quadrats at South East Bay and Tikitikinahoa also increased in total basal area (65.71 and 40.48 $m^2 ha^{-1}$ respectively). Conversely the quadrat located at Panui Peninsula had a slight decrease of 2.43 $m^2 ha^{-1}$; this is attributed to a large loss of *Metrosideros* stems due to self-thinning.

The density of live *Metrosideros* stems was related to stand age; stem density of *Metrosideros* decreased between the initial measurement and re-measurement in all four quadrats (Figure 5.9). *Metrosideros* stems decreased on an average rate of 6.2 stems ha $year^{-1}$; however this was much greater in the Panui Peninsula quadrat, where the rate exceeded 15 stems ha^{-1} $year^{-1}$. This result confirms data from previous analysis (Chapter Four) that self-thinning of *Metrosideros* stems is far more prevalent in the first 60 years of forest development. The basal area of *Metrosideros* increased in all quadrats except Panui Peninsula, where the large loss of *Metrosideros* stems resulted in a minor decrease of 2.6 $m^2 ha^{-1}$. The basal area of *Metrosideros* in all other quadrats increased at an average rate of 35.5 m^2 ha^{-1}.

The presence of *Litsea* also appeared to be related to stand age; this species was not present in the Motuotau quadrat and only juveniles (<2 cm dbh) were present in the Panui Peninsula quadrat at the time of re-measurement. Both of these quadrats were estimated to represent forest <70 years old. The future arrival of *Litsea* in the Motuotau quadrat maybe hindered due to a single large *Litsea* tree, representing the only seed source on the island, having died in the time period between surveys. However, in the time period between measurement of the Tuhua quadrats, *Litsea* had become prolific in the understory of Tikitikinahoa and South East Bay stands (both stands estimated to be >100 years old), whereas the species had not proliferated in the much younger quadrat located near Panui Peninsula (c. 80 years old).

Other shade tolerant species which also increased in abundance in the Tuhua quadrats were *M. excelsum*, *P. arboreus*, *Vitex* and *Dysoxylum*. The later two species were present predominantly as juviniles (<2 cm dbh); however the large number of saplings suggest the species are likely to persist. The number of species present in the Motuotau quadrat was much lower than that in the Tuhua quadrats, and generally all species present (stems >2 cm dbh) increased in basal area, particularly *P. lessonii* which increased from 3.35–7.80 $m^2 ha^{-1}$, this increase was coupled with an increase in density from 1042–1225 stems ha^{-1}.

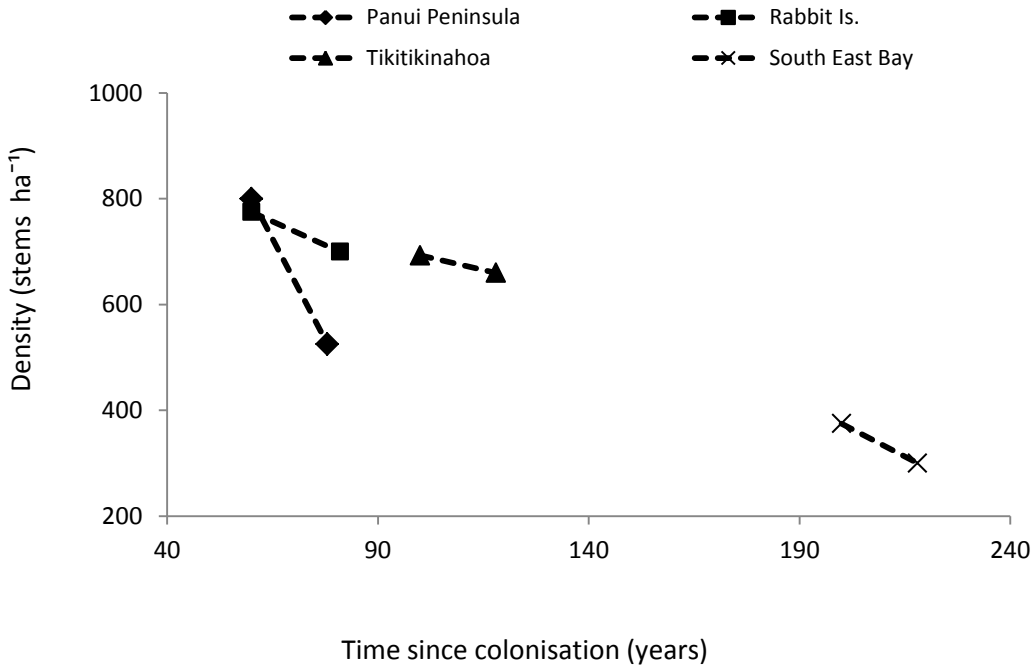


Figure 5.9: *Metrosideros excelsa* stem density (stems ha^{-1}) in permanent quadrats located on Mayor Island (Panui Peninsula, Tikitikinahoa and South east Bay) and Motuotau, at the time of quadrat installation (T1) and at the time of re-measurement (T2). Stand ages estimated from diameter-age relationship.

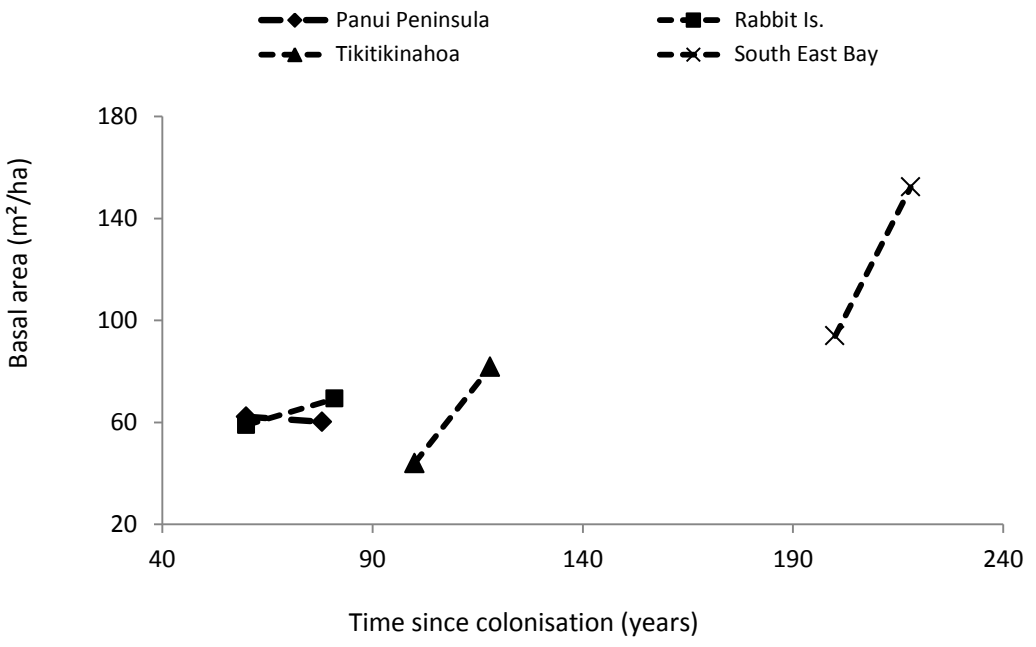


Figure 5.10: *Metrosideros excelsa* basal area (m^2 ha^{-1}) in permanent quadrats located on Mayor Island (Panui Peninsula, Tikitikinahoa and South east Bay) and Motuotau, at the time of quadrat installation (T1) and at the time of re-measurement (T2). Stand ages estimated from diameter-age relationship.

Table 5.5: Species stem density (stems ha^{-1}) in permanent quadrats on Tuhua (Panui Peninsula, Tikitikinahoa and South east Bay) and Motuotau, at the time of quadrat installation (T1) and at the time of re-measurement (T2).

Species	Tuhua						Motuotau	
	Panui Peninsula		South East Bay		Tikitikinahoa			
	T1	T2	T1	T2	T1	T2	T1	T2
Aristotelia serrata	-	-	25	-	33	-	-	-
Coprosma lucida	500	1025	-	-	67	-	-	-
Coprosma grandifolia	50	-	-	25	-	-	-	-
Coprosma macrocarpa	1050	2150	1225	1150	133	867	-	-
Coprosma repens	-	-	-	-	-	-	2714	1450
Corynocarpus laevigatus	-	-	-	25	-	-	-	-
Dysoxylum spectabile	-	-	-	-	-	33	-	-
Entelea arborescens	-	-	-	-	-	100	-	-
Geniostoma rupestre	400	475	-	25	-	-	-	-
Knightia excelsa	-	25	75	75	133	100	-	-
Litsea calicaris	-	-	75	775	33	1600	-	-
Hedycarya aborea	-	-	50	925	-	100	-	-
Macropiper excelsum	150	700	200	1075	67	2033	-	-
Melicytus ramiflorus	100	150		175	167	333	-	-
Melicytus novae-zelandiae	-	-	-	-	-	-	-	50
Metrosideros excelsa	800	525	375	300	733	667	775	675
Metrosideros excelsa dead	175	150	75	50	267	-	-	100
Myrsine autralis	1125	1150	495	400	2600	1433	-	-
Pittosporum crassifolium	-	50	-	-	-	-	150	50
Pseudopanax arboreus	50	175	-	50	-	200	-	-
Pseudopanax lessonii	-	-	25	75	-	-	1042	1225
Vitex lucens	-	25	-	25	-	-	-	-
Total Density	4400	6600	2620	5150	4233	7467	4681	3550

Table 5.6: Species basal area (m^2 ha^{-1}) in permanent quadrats on Tuhua (Panui Peninsula, Tikitikinahoa and South east Bay) and Motuotau, at the time of quadrat installation (T1) and at the time of re-measurement (T2).

Species	Tuhua						Motuotau	
	Panui Peninsula		South East Bay		Tikitikinahoa			
	T1	T2	T1	T2	T1	T2	T1	T2
Aristotelia serrata	-	-	0.01	-	0.15	-	-	-
Coprosma lucida	0.21	0.50	-	-	0.16	-	-	-
Coprosma grandifolia	0.00	-	-	0.10	-	-	-	-
Coprosma macrocarpa	0.85	2.10	0.63	1.63	0.56	0.28	-	-
Coprosma repens	-	-	-		-	-	0.68	5.88
Corynocarpus laevigatus	-	-	-	0.05	-	-	-	-
Dysoxylum spectabile	-	-	-		-	0.04	-	-
Entelea arborescens	-	-	-		-	0.15	-	-
Geniostoma rupestre	0.19	0.11	-	0.01	-	-	-	-
Knightia excelsa	-	0.17	2.51	2.90	10.79	9.37	-	-
Litsea calicaris	-	-	0.02	0.55	0.02	1.30	-	-
Hedycarya aborea	-	-	0.02	0.94	-	0.04	-	-
Macropiper excelsum	0.32	0.21	0.14	1.67	0.23	3.73	-	-
Melicytus ramiflorus	0.63	1.30	-	0.87	0.58	1.25	-	-
Melicytus novae-zelandiae	-	-	-	-	-	-	-	0.05
Metrosideros excelsa	63.30	60.17	93.94	152.31	47.31	82.56	29.47	66.96
Metrosideros excelsa (d)	2.74	3.82	1.45	3.63	1.66	-	-	2.15
Myrsine autralis	5.09	2.39	1.41	1.02	8.09	6.24	-	-
Pittosporum crassifolium	-	-	-	-	-	-	0.33	0.05
Pseudopanax arboreus	0.01	0.04	-	0.03	-	0.06	-	-
Pseudopanax lessonii	-	-	0.01	0.09	-	-	3.35	7.80
Vitex lucens	-	0.09	-	0.01	-	-	-	-
Total Basal Area	73.36	70.93	100.14	165.85	69.55	105.03	33.83	82.90

5.5 Discussion

5.5.1 Regeneration strategies of major species

Metrosideros diameter frequency distributions suggested that Bay of Plenty forests were within four distinct phases of forest development, and these represent a continuum from high density young stands, to mature forest, and subsequently forest where shade-tolerant species were becoming prominent in the canopy. Considering the life span of *Metrosideros*, stem growth rates deduced in Chapter Three, and the moribund state of trees, it is expected many *Metrosideros* encountered in the >300 year stands will die out within the next few decades.

The diameter frequency distributions observed for key species, also suggest that appreciable shifts in species composition are occurring and thus *Metrosideros* forests in the Bay of Plenty are not in a steady state, but instead at different phases of forest succession. The replacement strategies among major species involve the establishment at different phases of forest development, and this directly relates to species' shade tolerances. Without further disturbance, much of the *Metrosideros* forest in the Bay of Plenty will progress towards a community type dominated by species which are able to regenerate and replace themselves beneath a closed canopy (i.e., species which have even aged population structure), with smaller contributions of species reliant on canopy gap formation.

Kunzea and *Metrosideros* juveniles were the most light-demanding of all tree species sampled, and consequently their regeneration was generally restricted to open sites and gave rise to cohort populations. *Kunzea* is generally considered seral, and is usually successively overtopped by taller shade tolerant species (Esler & Astridge 1974; Smale 1994). However, some regeneration of *Kunzea* was occurring in older *Metrosideros* forests, juveniles were mostly suppressed and based on their high light requirements (Chapter Four), would probably require gap formation for further development.

Clarkson & Clarkson (1994) were the first to publish *Metrosideros* diameter frequency data, however this focussed specifically on Whakaari forest. Almost pure stands of *Metrosideros* there also exhibited cohort population structures, with the exception of one stand located at Ohauora, which displayed a reverse-J curve structure; indicating more recent establishment. In contrast to forests

sampled during this study, Whakaari stands had higher proportions of dead stems, and these were of varying diameters; a result of the on-going volcanic disturbance, most likely toxic fumes, wet ash coating leaves and "acid rain".

Sites of *Metrosideros* regeneration were uncommon in the Bay of Plenty; this is in part due to *Metrosideros* requiring landscape-scale disturbances (e.g. fire or volcanic eruption) to initiate regeneration and such disturbances do not frequently occur. Smaller scale disturbance events such as landslides are common in the region, and provide suitable regeneration conditions, however, timing is crucial because *Metrosideros* seeds do not form a persistent seed bank and germination must occur soon after seed fall, usually March-April. Interestingly, a landslide which occurred within *Metrosideros* forest at Matata Scenic Reserve during February 2011, hosted no *Metrosideros* seedling until late-February the following year (pers. obs.). The initial absence of *Metrosideros* seedlings may have been due the presence of loose and unconsolidated rubble which was removed in the following months by further wind and rain induced erosion. All *Metrosideros* seedlings observed in this study were growing upon rocks or on hard and fissured substrates, demonstrating the species affinity for primary substrates.

Diameter frequency distributions of mid-successional species *Litsea* and *Corynocarpus*, and mid-late successional *Dysoxylum* and *Beilschmiedia*, combined with shade-tolerance data (Chapter Three), suggest these species are capable of continued recruitment in the understory of mature *Metrosideros* forest. The population structure of *Beilschmiedia* has been well documented (Smale & Kimberley 1983; Ogden 1985) and often shows an all-sized population in mature forest; the reverse-J curve observed in mature (>300 years) *Metrosideros* forest indicates a recent establishment and it likely the precursor to an even aged population in the decades to come.

5.5.2 Successional models and trajectories

Using results from the present study, a generalised model of *Metrosideros* forest succession has been developed (Figure 5.11). This model had many parallels to Percy's (1952) and Atkinson's (2004) models of succession following fires on the northern offshore islands (New Zealand). In the Bay of Plenty, following a disturbance (e.g. fire or landslide), young high density, pure or mixed *Metrosideros* forest establishes (c. 30 years). Other primary immigrants may

include *Kunzea* and *Leptospermum*, which also have small wind-dispersed seeds and high light requirements. These species are however less tolerant of coastal conditions, and have shorter life spans, thus may only persist in semi-coastal and inland localities for approximately 200 and 100 years respectively. Atkinson (2004) suggests *Metrosideros* and *Kunzea* grow together as mosaics of contrasting stands, rather than mixtures, however both combinations were observed in this study (Matata Scenic Reserve and Great Barrier Island, respectively).

Within the first 60 years of forest development, six predominantly bird-dispersed, secondary forest immigrants commonly establish and contribute to the forest understory. These are *Myrsine*, *Pseudopanax lessonii*, *Pseudopanax arboreus*, *Melicytus ramiflorus*, *Geniostoma*, and *Macropiper excelsum*. Seedlings of all six species are considered shade-tolerant; species occupy intermediate light environments relative to those occupied by early colonists (e.g. *Metrosideros*) and later successional species (e.g. *Beilschmiedia* and *Dysoxylum*). Of these species, *Myrsine* was more prevalent in semi-coastal locations whereas the *Pseudopanax* spp. and *Melicytus ramiflorus* were more prevalent in coastal locations. Atkinson (2004) also noted *Myrsine* was more common beneath *Metrosideros* in sheltered localities, whereas *Melicytus ramiflorus* was more common beneath *Metrosideros* on seaward facing slopes. This trend is attributed to the damaging effects of salt laden winds, from which, *Melicytus ramiflorus* recovers more hastily and thus

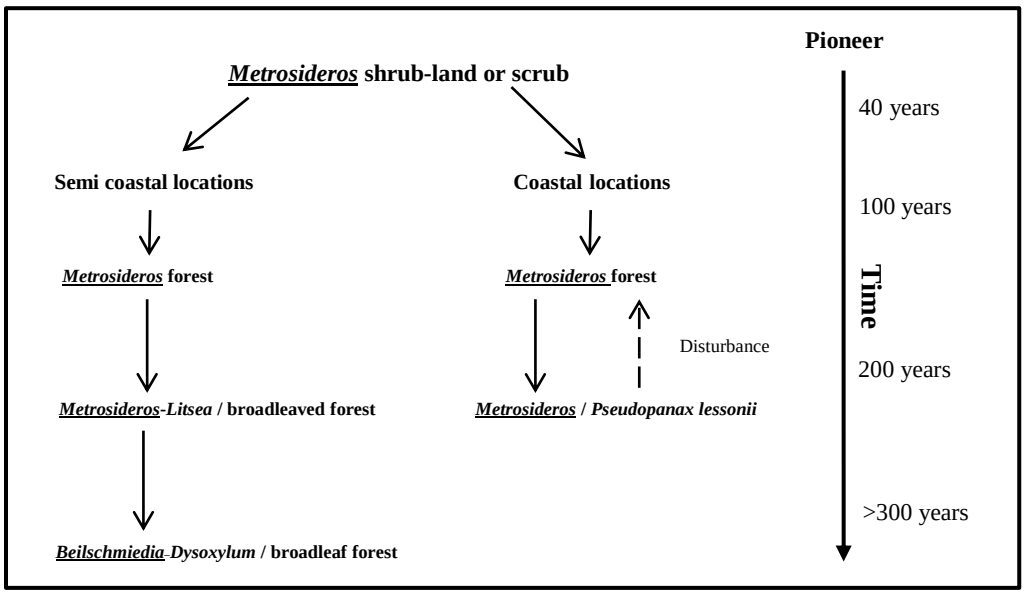


Figure 5.11: Schematic summary of *Metrosideros* forest succession in relation to time, for forest in the Bay of Plenty Region. Note time scale is approximate.

competitively excludes *Myrsine* from the seaward facing areas (Atkinson 2004). These early successional understory species also commonly arrive in North Island *Kunuka* successions after approximately 60 years of development and all have broadly similar lifespans (Smale 1993; Atkinson 2004). Thus this suite of species is expected to die out of *Metrosideros* understories 80–180 years after establishment, and accordingly the presence of these species was detected to be much lower in mature *Metrosideros* stands.

Mid-successional tree species that arrived following c. 60 years of forest development included *Vitex*, *Corynocarpus*, *Litsea* and *Dysoxylum* however only the latter two were common and wide-spread. In the absence of future disturbance, *Beilschmiedia*/broadleaved forest is likely to represent the stable forest association, succeeding *Metrosideros* forest in semi-coastal localities.

Dysoxylum, *Litsea* and *Corynocarpus* are also likely to be a components the forest canopy, however because the continued replacement of these species may rely on canopy-gap formation (Chapter Four) they are less likely to reach densities attained by *Beilschmiedia*. Smale & Kimberley (1983) have assessed the regeneration patterns in *Beilschmiedia* dominated forest at Rotoehu, central Bay of Plenty**.** Forest composition was similar to that predicted to follow *Metrosideros* forest and the regeneration patterns observed were also consistent with the finding of this research. Smale & Kimberley (1983) found *Litsea* and *Knightia* juveniles rarely reached maturity in the forest under-storey and this was attributed to the species' light requirements. Conversely, *Dysoxylum* and *Beilschmiedia* were both capable of self-replacement, however this tended to favour *Beilschmiedia*, allowing the species to gain and retain canopy dominance.

This generalised model of *Metrosideros* forest succession is similar to that of coastal and semi-coastal *Metrosidersos polymorpha* successions, occurring on the Hawaiian lava flows. These two species are closely related, and both are primary colonisers of volcanic substrates (e.g. both aa and pahoehoe lava flows). *Metrosidersos polymorpha* however, has a considerably shorter life span. Atkinson (1970) & Clarkson (1997) report that within 400 years and following self-thinning, a closed-canopy forest (c. 20 metres in height) dominated by *M. polymorpha* is possible and this hosts an understory of shade-tolerant species, especially treeferns (*Cibotium* spp.) In the most mature forests, formed upon

prehistoric lava flows, *Metrosidersos polymorpha* has been completely replaced by shade tolerant species (e.g. *Diospyros sandwicensis*, *Myoporum sandwicense* and *Sophora chrysophylla*).

The New Zealand species *Metrosideros kermadecensis* and *Metrosideros umbellata* are also early colonists and forests dominated by these species share features with *Metrosideros excelsa* forest. *Metrosideros kermadecensis* is endemic to the Kermadec Islands, where the species colonises recent volcanic surfaces and forms pure even-aged stands, which reflect the islands volcanic history (Atkinson 1970; Simpson 2005). *Metrosideros umbellata* is widespread throughout much of the South Island, and is an early coloniser of rocky surfaces created by debris flows and landslides and glacier moraine (Atkinson 1970). As for *Metrosideros excelsa*, the species forms high density, cohort stands within 60–100 years of development, and these also undergo natural self-thinning. In constats, podocarps (*Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Podocarpus hallii*) rather than broadleaved species, eventually establish beneath, and replace *Metrosideros umbellata* in the canopy (McKinzey 2004; Simpson 2005).

Unlike the directional succession previously discussed, *Metrosideros* forest located on coastal headlands in the Bay of Plenty region is more prone to disturbances, such as cliff collapse and landslides (Figure 5.12), thus in such locations *Metrosideros* forest is likely to have a cyclic succession. Cyclic *Metrosideros* succession is particularly evident in a small forest stand, which inhabit a 1–2 km coastal cliff, near the Paparoa reef, Taranaki. *Metrosideros* populations there have become an integrated part of the erosion cycle and no trees are older than c. 300 years due to the frequent erosion (Benson 1995; Simpson 1997).

It has been remarked that the greatest contemporary influence on indigenous forest succession is introduced herbivores (Smale & Smale 2003), and *Metrosideros* forest maybe no exception. The Orokawa and Homunga Bay stands had the most severe browsing damage of all study sites; mid successional and mature stands within these reserves did not contain *Litsea*, nor was it observed in the wider area. Conversely, *Litsea* was prolific on Tuhua (pest free), situated just offshore. *Litsea*, while certainly not a threatened species, is experiencing a decline in some parts of its range. The death of apparently healthy trees is often reported

Figure 5.12 Photograph on left shows the path of a landslide in Matata Scenic Reserve that occurred in February 2011; Photograph on the right shows a collapsed cliff within *Metrosideros excelsa* forest at West End beach, Ohope, July 2011.

and the cause is unknown. However, the absence of *Litsea* in some stands may also be attributed to herbivore browse and lack of a nearby seed source. In seedling field trials conducted in Waikato forests, Overdyck (unpubl data.) found *Litsea* germination was greatly reduced in the presence of possums and other grazers compared to germination in pest free enclosures; only 6.3 of seeds sown in unprotected areas germinated, and these did not survive to maturity due to seedling predation. *Litsea* fruits, like those of *Dysoxylum* and *Beilschmiedia* are primarily dispersed by bird. It is widely known that *Beilschmiedia* and *Dysoxylum* fruit, flowers and leaves are severely browsed in the presence of possums (Buddenhagen & Ogden 2003; Ecroyd & Jones 1997).

The majority of the Bay of Plenty reserves have intensive pest control and monitoring schemes, and these have been successful in reducing pest numbers (Environment Bay of Plenty 2009). However, if pest control was to cease, death of *Metrosideros* trees and a reduction in the regeneration of palatable species is expected (e.g., *Litsea*, *Beilschmiedia* and *Dysoxylum*), altering the forests future composition.

5.6 Conclusion

The present study provides the first quantitative analysis of successional patterns within *Metrosideros* forest, in the Bay of Plenty Region. The approach used here, quantifying regeneration in four consecutive phases of forest development, has allowed *Metrosideros* forest dynamics and successional trajectories to be

determined. Although this research focussed on forests in the Bay of Plenty Region, comparison with previous studies (Percy 1956; Clarkson & Clarkson 1990; Atkinson 2004) suggests results are probably consistent with *Metrosideros* forest in the wider area. The replacement strategies among major species involved establishment at different phases of forest development and the order of establishment was strongly correlated species shade tolerance; with early succession species such as *Metrosideros* and *Kunzea* being the least shade tolerant and late successional such as *Beilschmiedia* and *Dysoxylum* species being the most shade-tolerant. Based on species shade tolerance and diameter frequency distributions, the forest type predicted to succeed *Metrosideros* forest in lowland and semi-coastal localities is one dominated by *Beilschmiedia*, due to this species ability to regenerate beneath its own canopy.

Chapter Six: Biological flora of New Zealand
Metrosideros excelsa (Sol. Ex) Gatertn. (Myrtaceae), pōhutukawa

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6.1 Abstract

Information relevant to the ecology, biology and conservation of *Metrosideros excelsa* (Myrtaceae) is presented and reviewed here. Information has been sourced from published and unpublished works. *Metrosideros excelsa* is an evergreen tree or shrub, endemic to coastal regions of northern New Zealand, and the North Island, Central Volcanic Plateau. *Metrosideros excelsa* is arguably the most well-known, iconic and cherished plant species in New Zealand, and is highly significant in both Māori and European cultures. The species is renowned for its sudden and spectacular mass flowering episodes, its gnarly and sprawling growth form, and its ability to survive in the most precarious and seemingly inhospitable environments. When in flower, trees are laden with brilliant red brush flowers, with each producing copious amounts of nectar that feeds native tui (*Prosthemadera novaeseelandiae*), bellbirds (*Anthornis melanura*), stitchbirds (*Notiomystis cincta*), short-tailed bats (*Mystacina tuberulata*) and bees (*Hylaeus* spp., *Leioproctus* spp., *Lasioglossum* spp.). Historically, *Metrosideros excelsa* has been significant in both Māori and European cultures, however, human induced burning and land clearance has seen the species decline. *Metrosideros excelsa* is a primary rock coloniser and has evolved mechanisms to tolerate drought, severe winds and salt spray, allowing it to establish and flourish in hostile environments. Despite this apparent robustness, this species is threatened by possum browsing, trampling by stock, and habitat loss.

Key words: biological flora; pōhutukawa; *Metrosideros excelsa*; ecology; succession; conservation; New Zealand

6.2 Morphological description

Metrosideros excelsa is a perennial evergreen woody shrub or tree. Mature trees can reach 20 m tall and trunks can be up to 2 m in diameter, often with a gnarly growth habit (Simpson 2005). Trees can be multi-stemmed, particularly in open sites and are frequently wider than they are tall because of dense and sprawling canopies. In a forest environment however, shading will result in a more upward growth form (Simpson 2005). Aerial roots are readily produced on the trunks and branches of some trees and these grow towards the ground, where they may act to anchor the tree and increase access to nutrients and water. Branching is sympodial and spreading, branchlets are stout, and young shoots are often densely tomentose. Bud scales are nearly always present (Allan 1961). Leaves are coriaceous, thick and clad with tomentum on the lower surface; however young leaves are glabrous, particularly on juvenile plants. Leaves are decussate, usually opposite, and are positioned on short, stout petioles. Lamina dimensions vary, but generally range from 2.5–5 cm in width and 5–10 cm in length; shade leaves are typically at the higher end of this spectrum. Leaf shape can range from elliptic to oblong and possess either acute or obtuse leaf tips. Inflorescences are auxiliary and terminal (terminate in groups of three flowers) and are composed of broad compound cymes (Dawson 1968); a single inflorescence is composed of c. 14 flowers. Pedicels are stout and tomentose (Allan 1961). Flowers are formed by a 'brush' of stamens; these are crimson to scarlet in colour, and occasionally yellow (Bergin & Hosking 2006). Petals are insignificant, oblong and persistent (Dawson 1968).

6.2.1 Inflorescence

Metrosideros excelsa has compound inflorescences in the form of dense panicles. Individual flowers are borne on cymes, in sets of three, collectively termed cymules. Cymules are arranged in opposite pairs (Dawson 1968). *Metrosideros excelsa* flowers are the largest of all New Zealand *Metrosideros* species; a single inflorescence comprises an average of 14 flowers. However, the spectacular floral display is not due to petals, which are insignificant and persistent (Figure 6.2b), but instead, bright crimson stamens (Wotherspoon 1993). Each flower has approximately 27 stamens, however this is highly variable. Stamens are between 20 and 37 mm in length, and positioned around a nectar cup (Woothersoon 1993).

Flower buds are terminal (beyond leaves); consequently flowers are conspicuous and often obscure canopy foliage (Simpson 1994). Each flower contains a 3-locular semi-superior ovary, which in turn, contains more than 900 ovules (Schmidt-Adam & Murray 2002).

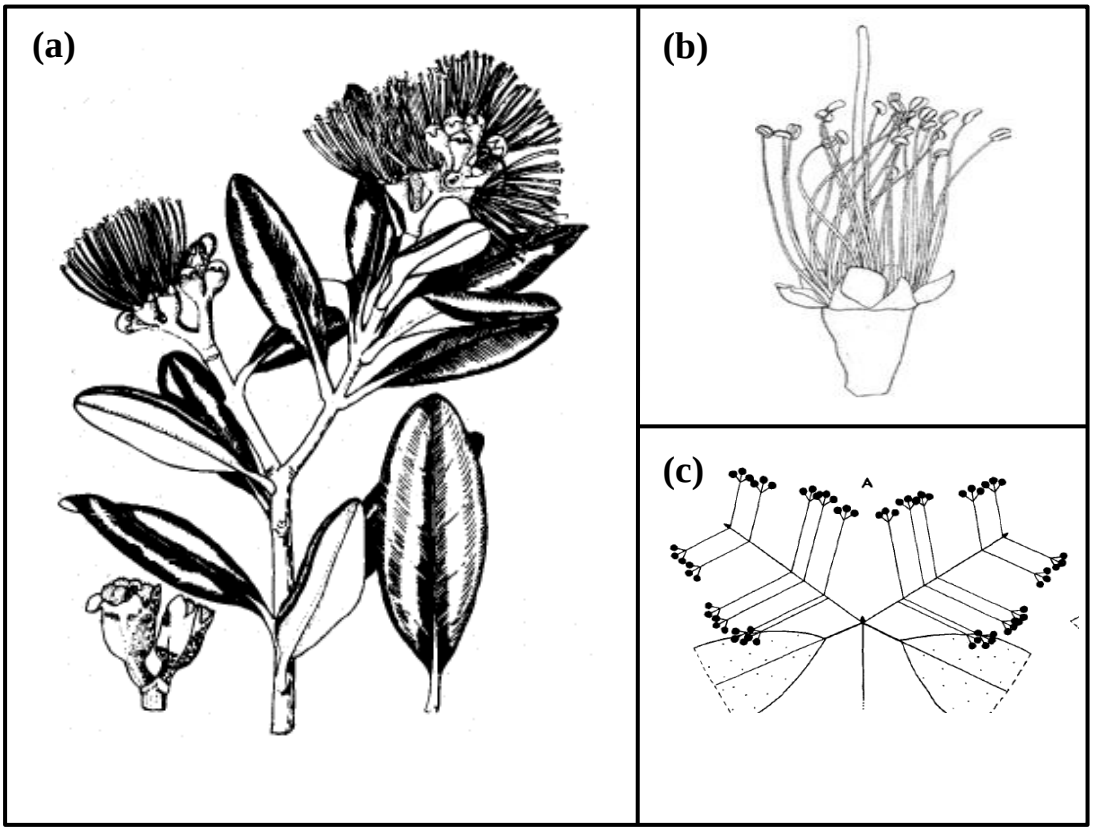

Figure 6.1: (a) Morphological features of *Metrosideros excelsa* (from Poole & Adams 1994). **(b)** *Metrosideros excelsa* flower; sepals, petals and anthers (modified from Dawson 1967). **(c)** *Metrosideros excelsa* flower and inflorescence arrangement (modified from Dawson 1967).

6.2.2 Stigma and style

The stigma and the style of the *M. excelsa* flower provide the male gametophyte access to the flower ovaries. Following the classifications of Boland & Sledgley (1986) the stigma type possessed by *M. excelsa* can be described as blunt and uniform; this is the common stigma type of many eucalypts, also in the family Myrtaceae (Schmidt-Adam & Murray 2002). In cross section, the stigma is approximately circular and has an average diameter of 0.62 mm. Stigmatic papillae line the stigma, these are unicellular and lack a cuticle. Extracellular secretions of the papillae are high in lipids and possibly represent an adaptation to protect against desiccation in the dry and windy coastal environments which *M. excelsa* commonly occupies. Lipids may also aid in trapping pollen. In the

stigma, pollen tubes grow down between stigmatic papillae (Schmidt-Adam & Murray 2002).

The diameter of the style increases basipetally, reaching an average of 0.74 mm near the ovaries. Styles comprise an epidermis with outer cuticle (2–4 µm thick), parenchymous cortex and a central transmitting tissue/tract. The transmitting tract cells are loosely arranged and form a mosaic with large intercellular spaces, which are filled with secretion products (Schmidt-Adam & Murray 2002). Prior to fertilisation, pollen tubes growth down through these intercellular spaces, before reaching the flower ovaries (Figure 6.2a).

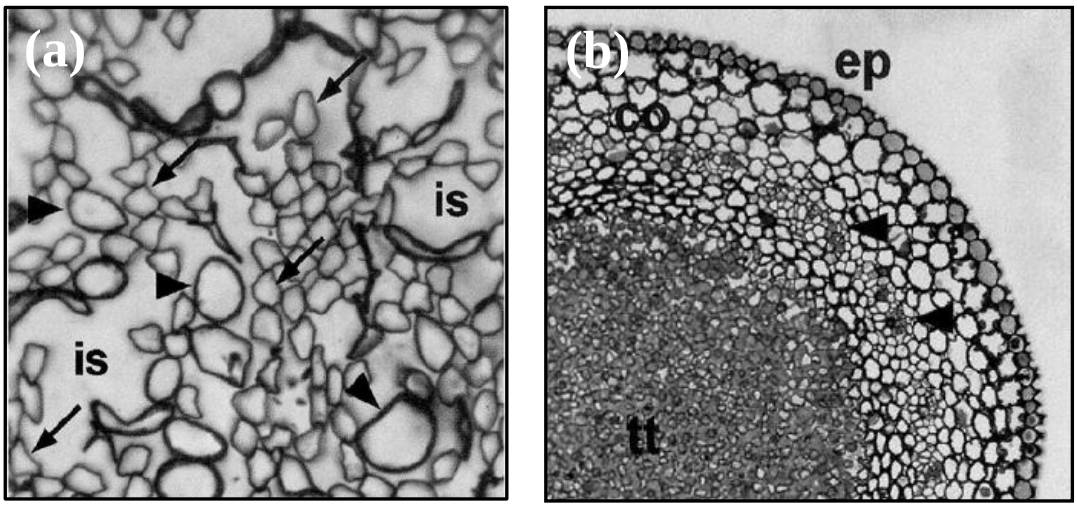

Figure 6.2: (a) Transverse section through pollinated style of *Metrosideros excelsa*. Arrow heads show transmitting tract cells, (is) intercellular substance. **(b)** Bright field micrograph of an un-pollinated style. tt = transmitting tract, ep = epidermis, co = cortex, arrows point towards vascular bundles (images from Schmidt-Adam & Murray 2002).

6.2.3 Leaf

The leaves of *M. excelsa* have features to protect against harsh coastal conditions. Emerging autumn leaf buds are covered in protective bud scales while spring leaves are covered in white tomentum. This tomentum wears off the upper leaf surface with time but persists and thickens on the underside; reducing water loss and protecting the stomata from the effects of salt laden winds (Simpson 2005).

Examination of *M. excelsa* leaf cross-sections show that the tissues are notably differentiated (Figure 6.3). A thick cuticle layer consisting of a hard inert waxy material that is excreted from the epidermal cells screens the upper leaf surface. The cuticle is markedly thicker in the leaf margins, where it is expected that insect

attack would begin (Simpson 2005). Hairs possessed by adult *M. excelsa* leaves protrude from the epidermal cells. Below the epidermal cells there is an adjacent and thick layer of hypodermis or water-filled cells (3–4 cells thick); these are particularly thick around the mid-rib and main veins, and are likely to be an adaptation to drought (Simpson 2005). Beneath the hypodermis is a layer of vertically elongated palisade cells, where chlorophyll is predominantly concentrated. The lower third of the lamina is composed of spongy mesophyll and many air spaces; where gas-exchange takes place. However, air pockets are generally not abundant, making the mesophyll and palisade layers difficult to distinguish. Vascular tissue lies within the mesophyll layer, and these are supported by fibrous tissues. Leaves also contain oil glands, each an approximately circular cavity lined with secretory cells. The function of these may be the production of compounds to discourage browsing animals and fungal growth (Simpson 2005). The lower epidermis has a thick cuticle, comparable to that on the upper leaf surface. Hardened crystals are scattered throughout the leaf tissues that the hardness of these crystals may act to discourage insect browse (Simpson 2005).

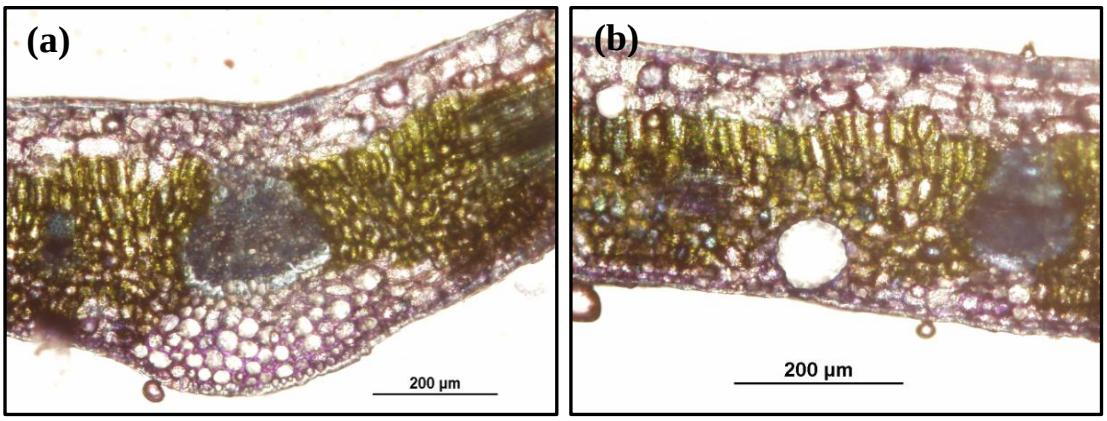

Figure 6.3: Sections across blade of *Metrosideros excelsa* leaf. **(a)** Shows main mid-rib and vascular tissue. **(b)** shows secondary vein; large cavity is likely to be an oil gland.

6.2.4 Roots

An important characteristic of *M. excelsa* is its ability to form roots from almost any part of the tree and at any stage of maturity. Some individual trees produce large quantities of adventitious roots while others relatively few; this trait is thus likely to be genetically controlled, though this is not well understood (Simpson 2005). Adventitious roots enable the *M. excelsa* to traverse open ground,

penetrate fissured rock, and can enter the ground to form props (Dawson 1967; Dawson & Sneddon 1969) and these abilities are vital when occupying coastal cliffs and colonising fissured lava fields (Simpson 2005). Adventitious roots continue to be formed by adult trees, particularly by those which have damaged canopies or are severely leaning; this is a suspected response to imbalance and results in a strengthening of the trunk (Simpson 2005). Adventitious roots also enable *M. excelsa* trees to cling to cliffs, or descend from cliffs and anchor into the soil below; branches are able to bend of rotate over the cliff edge for decades, producing new adventitious roots which penetrate the substrate, providing additional support (Dawson 1967; Bergin & Hosking 2006).

6.2.5 Wood

All members of the genus *Metrosideros* are renowned for the hardness and durability of their wood. The features of *Metrosideros* wood, which underlie this trait, include:

- An abundance of parenchyma cells which store carbohydrates and resins;
- Wide rays (≥3 cells thick) arranged in sheets radiating across the wood;
- A dominance of thick wall fibres, comprised of narrow elongated cells and densely packed around phloem vessels (Simpson 2005).

The wood has a swirled grain and is very dense. Annual stem growth rings are described by Meylan & Butterfeild (1976) as indistinct to slightly distinct. The heartwood of *Metrosideros* has a rich reddish brown colouration, often with black or pinkish streaks, and although it has been suggested the heartwood of *M. excelsa* is resistant to fungi, heartwood often has a decayed centre, and this is most likely due to attack by wood-rooting fungi (Bergin & Hosking 2006).

6.3 Chemistry

A number of chemical substances have been identified in the tissues of *M. excelsa.* Anthocynins are water-soluble, vacuolar flavonoids (Solangaarachchi & Gould 2001) responsible for the red colouration of *M. excelsa* flowers. Anderson (1988) identified seven distinct Anthocynins in the flower tissue of *M. excelsa,* and these were:

- Delphinidin-3-glucoside
- malvidin-3-glucoside
- cyanidine-3-glucoside
- Petinidun-3-glucoside
- peanindin-3-glucoside
- cyanidine-3,5-diglucoside
- malvidin-3,5-diglucoside

Anthocyanin pigmentation is also a prominent feature in the adventitious roots of *M. excelsa*. They are present in one or more cell layers of the root cap, epidermis, hypodermis and cortex. Anthocyanins in the root tissues tend to be cyanidin and delphinidin based. Light exposure is important in the production of these pigments, thus they are more abundant in the outer-most root layers. The location of these pigments in sun exposed regions has led to the inference that they may serve to protect against UV-B radiation. However, the role of anthocyanins in adventitious roots is still relatively unknown (Solangaarachchi & Gould 2001).

Flavonoids have also been isolated in *M. excelsa* tissues; these are known to have a large array of functions, including pigmentation and protection (Cushnie & Lamb 2005). Most plant flavonoids have oxygenated B-rings; however five unusual C-methyl flavonoids with no B-ring oxidation have been identified in *M. excelsa* tissues. Mustafa et al. (2005) have shown 5,7-dihydroxy-6,8-dimethylflaanone is the major flavonoid constituent of *M. excelsa* leaves, whereas 2,6-dihhydroxy-3-methy-l-4-methoxychalcone dominates capsules, flowers, buds, twigs and seed. Juvenile flower buds have extremely high levels of flavonoids; at such levels these may have protective properties and defend the vital reproductive organs from bacterial/fungal attack (Mustafa et al. 2005).

6.4 Geographic distribution

Metrosideros excelsa is one of New Zealand's "latitude 39" plants (Figure 6.4), like many other indigenous species (*Agathis australis*, *Phyllocladus toatoa* and *Beilschmiedia tarairi*) *Metrosideros excelsa* is generally limited to the warm temperate zone, north of this latitude (Simpson 2005). Below this latitude, suitable environments are often inhabited by other members of the genus, such as *M. robusta* and *M. umbellata.* *Metrosideros excelsa* is a coastal species and at the time of European settlement, formed a continuous belt around the north of the North Island; stretching from Urenui on the west coast to Gisborne, or possibly Young Nick's Head, on the east coast (Simpson 2005; Bergin & Hosking 2006).

The southern limits of the species have since retreated north and currently extend no further than Wai-iti and Mawhia Point, on the west and east coasts, respectively. The species has an infrequent occurrence from Wai-iti to Manukau Harbour on the west coast, which may be explained by unsuitable mudstone substrates. Logging, accidental fire and land clearance have reduced the distribution of *M. excelsa* to small fragmented populations and scattered isolated trees, primarily on cliff tops and coastal banks (Bergin & Hosking 2006).

Northern New Zealand islands may provide the best examples of original *M. excelsa* forest, including natural plant and animal associations. *Metrosideros excelsa* forest is a major vegetation type on islands such as the Poor Knights Island group, Little Barrier Island, Mayor Island, and Rangitoto (Simpson 2005). White Island, off the coast of Whakatane, provides the only present day example of forest change in response to on-going volcanic disturbance (Clarkson & Clarkson 1994). Inland *M. excelsa* forest also exists; these are primarily on the Central Volcanic Plateau; where *M. excelsa* stands border Lake Rotorua and Taupo, and form a series of smaller stands along the Tarawera River (Simpson 2005).

There is debate as to the origins of the inland *M. excelsa* populations. Some believe they originate from Māori plantings and have subsequently spread into the wider landscape (Bergin & Hosking 2006); *Metrosideros excelsa* flowers are highly valued by Māori people, the red coloration is considered chiefly and worn by individuals with high rank, thus Māori often transplanted *M. excelsa* outside of their natural range. As a result trees also exist in areas such as Wellington and the Marlborough Sounds (Bergin & Hosking 2006). However, the presence of other coastal species on Central Volcanic Plateau, particularly in the Rotorua lakes Region, suggests that the remaining inland *M. excelsa* stands are natural (Clarkson et al. 1991).

Metrosideros excelsa forest was likely to be far more widespread through inland localities, as a coloniser of new surfaces that were created by the late Pleistocene and early Holocene lava flows from the Okataina Volcanic Centre (Clarkson & Clarkson 1994). Present day sequences show that strong competition from other broadleaved species (*Weinmannia racemosa*, *Litsea calicaris* and *Beilschmiedia*

tawa) tend to confine *M. excelsa* forest to open or extreme sites (Clarkson & Clarkson 1994).

Metrosideros excelsa has been introduced to many other countries as a garden plant because of its attractive appearance. *Metrosideros excelsa* has thrived in countries with warm mild climates similar to New Zealand, such as Australia, California and South Africa. In such locations *M. excelsa* trees grows so vigorously that the species it is regarded as an invasive pest (Yeates & Williams 2006).

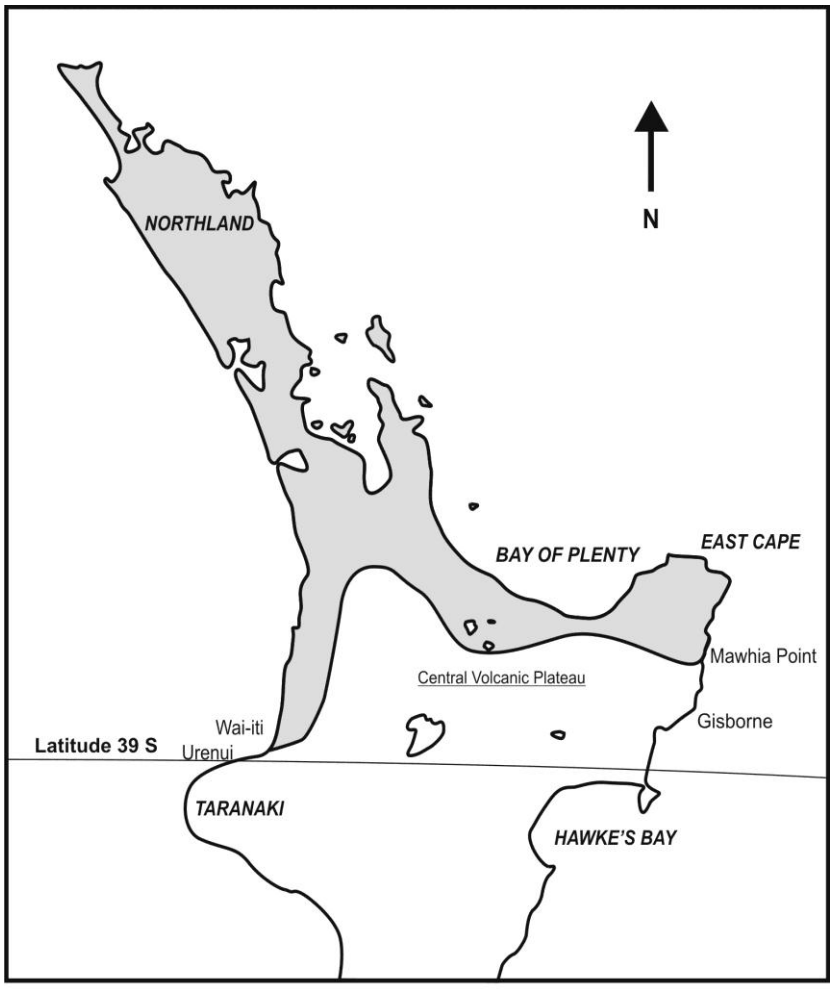

Figure 6.4: Generalised distribution of *Metrosideros excelsa* in New Zealand (modified from Simpson 2005)

6.5 Cytology

2n = 22 (Dawson 2008).

6.6 Nomenclature

The genus name *Metrosideros* was first used by Rumphius in 1743 to identify a group of hard-wooded timber trees in Indonesia. It was later re-applied to *Metrosideros collinia*, a timber tree from Tahiti, collected and lodged in 1769. The word *Metrosideros* is derived from the Greek terms *metra* meaning core or heart, and *sideron* meaning iron. Thus, *Metrosideros* species are often referred to as iron hearted trees, alluding to the durability and hardness of their timber (Simpson 2004).

Formerly *Metrosideros excelsa* was commonly referred to as *Metrosideros tomentosa* (A. Rich) in reference to the densely clad underside of mature leaves. The name *Metrosideros excelsa* was not formally given until 1788 (Allan 1961); excelsa means high, lofty or outstanding, a reference to the flowers position above the canopy foliage. *Metrosideros excelsa* was collected by Banks and Solander during Cooks first voyage to New Zealand (1769), and recorded as *Metrosideros excelsa*, notes on the sample plate read "*Calyx tomentosus, quinquedentatus, capsulae ad medium usque adnatus. Capsula ovata, extra calycem prominens, pubescens, trilocularis*" (Oliver 1928).

The Māori name "pōhutukawa" is thought to mean "splashed by the spray" an acknowledgement of the harsh coastal environment for which this species is superbly adapted (Riley 1994). The name "pōhutukawa" is mainly derived from the word "hutukawa" which is a head-dress of red feathers, an obvious reference to the species' profuse flowering episodes, which obscure the green foliage with crimson and red (Simpson 1994).

6.7 Taxonomy and relationships

Metrosideros excelsa is a member of the genus *Metrosideros,* subgenus *Metrosideros,* and belongs to the family Myrtaceae. Other taxa within this family, represented in New Zealand's endemic flora include: *Metrosideros* (subgenus *Mearnsia*); *Leptospermum*; *Syzygium*; *Lophomyrtus*; *Neomyrtus*. The genus *Metrosideros* contains approximately 50 described species (Sreekantan et al. 2001). These form a widely distributed and conspicuous component of the Pacific basin flora (Gardner et al. 2004), with representatives in the Philippines, New

Guinea, New Caledonia, New Zealand and many of the Pacific Islands. An outlying species is also present in South Africa (Anderson 1988).

It has been suggested by Dawson (1988) that the genus can be divided into two main subgenera; *Metrosideros*, the trees (generally found in the Pacific Islands) and *Mearnsia*, the vines (found on the rim islands of the western Pacific). New Zealand is home to 12 species of *Metrosideros;* six root climbing lianes, one shrub and five tree species (Dawson 1968). Common features of *Metrosideros* species include; the ability to occupy open rocky ground, preference of a warm temperate or subtropical climate, sensitivity to frost, the ability to form adventitious roots and the ability to establish on young soil with a low nutrient status (Simpson 2005).

Hybridisation between New Zealand's *Metrosideros* tree species is common. *Metrosideros excelsa* naturally hybridises with *M. robusta* as the species distributions commonly overlap. Hybrid populations are present in the Rotorua and Tarawera Lakes areas and also on Rangitoto Island (Cooper 1954; Clarkson 1990) and occasionally hybrid individuals are present among pure populations (Simpson 2005). *Metrosideros excelsa* and *M. kermadecensis* (Kermadec Island's pōhutukawa) also readily hybridise whenever they occur together in cultivation. Furthermore, *M. excelsa* is able to form hybrids with *M. umbellata* and *M. bartlettii*; however the distribution of *M. excelsa* and these two species less commonly overlaps (Simpson 2005). Hybridisation between species has raised concern about genetic pollution of natural stands (Simpson 2005), however genetic analysis has shown hybridisation has been an important factor in the evolution of the species (Gardner et al. 2004).

6.8 Biogeography

The genus *Metrosideros* is the most wide spread genus in the Pacific, with diversity centres in both New Zealand (with 12 spp.) and adjacent New Caledonia (16 spp.). However, New Zealand is the only landmass where late Palaeocene/early Eocene fossil pollen grains have been recorded. This, along with phylogenetic analysis suggests that New Zealand, rather than New Caledonia, is the landmass of origin and the source of the majority of *Metrosideros* taxa. Thus the New Zealand landmass is thought to be where the two subgenera (*Mearnsia*,

Metrosideros) first diverged, and the site where the sub genus *Metrosideros* was able to radiate and disperse (Wright et al. 2000). Further evidence for this includes the primitiveness of *Metrosideros umbellata*; based on DNA analysis *Metrosideros umbellata* is basal (Figure 6.5) to all other *Metrosideros* species (Wright et al. 2000).

All *Metrosideros* species, excluding *M. umbellata,* fall into three monophyletic clades (Figure 6.5). The first clade includes seven New Caledonian species as well as three species in western Oceania; these are likely to have dispersed from New Caledonia in the mid/late tertiary. The second clade contains six taxa from Melanesia and Samoa. The third monophyletic clade accounts for much of the total species range of subg. *Metrosideros*, this includes New Zealand species (*M. bartlettii, M. robusta* and *M. excelsa*) as well as all of the Polynesia taxa (Wright *et al.* 2000).

Wright et al. (2000) suggest there has been a minimum of four distinct dispersal events in the history of the *Metrosideros* subg. *Metrosideros*. An initial mid/late tertiary dispersal, from New Zealand to New Caledonia, followed by a mid/late tertiary dispersal from New Caledonia to the western Pacific, and again a mid/late tertiary dispersal from New Zealand to the south-western Pacific. And finally, the most recent and spectacular dispersal event is suggested to have occurred in the Pleistocene epoch, when the *Metrosideros* lineage dispersed from New Zealand to a number of islands in Oceania and remote Polynesia, where the subgenus is at the extreme of its

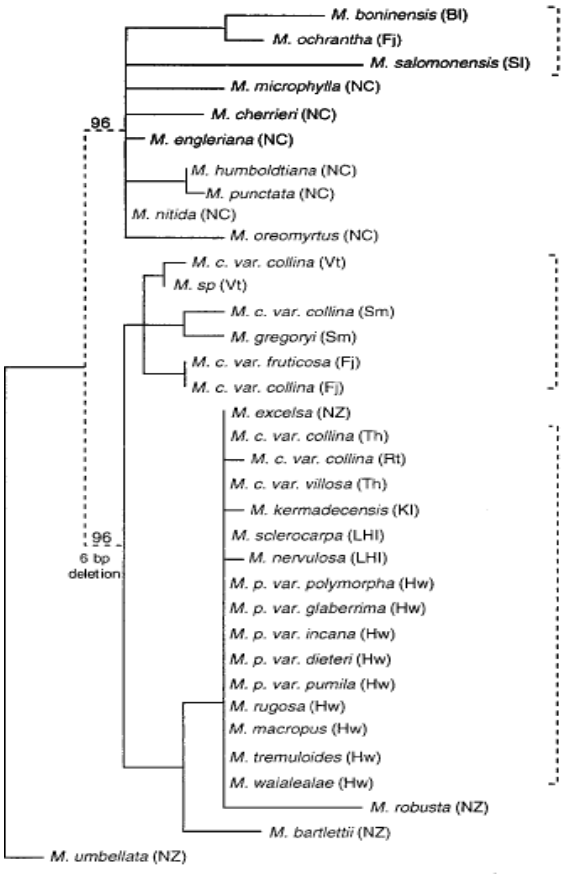

Figure 6.5: Consensus of parsimony analysis for 36 *Metrosideros* species. Solid lines indicate strict consensus, dashed lines indicate >90% consensus. Numbers refer to dispersal groups (modified from Wright et al. 2000).

range. This recent dispersal event has been interpreted as a result of climate change during the Pleistocene glaciations. The wind-dispersed species were able to take advantage of the powerful westerly weather systems and migrate across the hostile marine habitat (Wright et al. 2000).

6.9 Genetic structure

Two studies have investigated the genetic structure of remnant *M. excelsa* forests in New Zealand, and these have produced contradictory results. Gardner et al. (2004) applied chloroplast DNA sequencing to *M. excelsa* and other *Metrosideros* spp. from widespread New Zealand populations. Results indicated that across all species sampled, there was a greater diversity of haplotypes (groups of closely linked genes, usually inherited as a unit) in areas identified as glacial refugia. These areas included upper Northland, north-west Nelson and the Coromandel Peninsula. Gardner et al. (2004) interpret these findings as the result of range contraction, giving rise to isolated refuges during periods of cooler climatic conditions, followed by range expansion during warmer climates. The persistence of populations in isolated refuges is suggested to have given rise to greater haplotype diversity in the populations at these localities (Gardner et al. 2004).

A later study by Broadhurst et al. (2008) examined the genetic structure between and within ten populations of *M. excelsa*, using Amplified Fragment Length Polymorphism on genomic DNA. Results showed genetic differentiation among and within populations, but no evidence for a relationship between genetic structure and geographical location. Results also showed no evidence that areas proposed as glacial refugia had higher levels of diversity.

6.10 Reproductive biology

Floral cycles

Little is known of the seasonal patterns in floral development in *M. excelsa*, evidence suggests that floral induction takes place in autumn, in response to the shortening day length. Following flower initiation, reduced temperatures are thought to affect the ability of induced meristems to complete floral development; sub optimal temperatures may lead to flower bud abscission, and the reversion of terminal buds back to vegetative rather than floral growth (Sreekantan et al.

2001). Flowering intensity may be affected by proximity of buds to developing seeds during autumn (Henroid et al 2000); developing seeds may have an inhibitory effect similar to the suppressive effect *Malus* spp. fruit gibberellins have on floral induction (Sreekantan et al. 2001).

Flowering

Metrosideros excelsa is a mass flowering species, and flowers profusely for up to two weeks during December-January. Flowering episodes show high annual variation; *M. excelsa* populations often flower profusely one year and less obviously the next; this annual variation is not well understood, however, it is suggested that annual variation promotes cross pollination between populations (Simpson 1994; Bergin & Hosking 2006). During flowering, individual flowers remain open for 7 days; the timing of individuals within a population varies slightly (Schmidt-Adam et al. 2000). Each tree will produce an extensive number of flowers; this is thought to be in the range of 13,000 to 40,000 per flowering episode. Together, the showy crimson "brush" flowers form large inflorescences, and each individual flower produces an average 50 µl of nectar per day; 18 % (w/v) of the nectar is sucrose.

Flowers are hermaphroditic; they display an initial female phase (mean duration 1.3 days) followed by a longer hermaphrodite phase (mean duration 4 days), which is then followed by a further female phase. Stigmas remain receptive for a minimum of 9 days. However, during the final days pollination is rare, as pollinator rewards are depleted. Pollen has very high levels of viability (93.6%). Neither dichogamy; separation of gender phases by time, or herkogamy; separation by space, is important in preventing self-pollination during the hermaphroditic phase, when there is simultaneous display of pollen and stigma. The breeding system of *M. excelsa* is considered to be between facultative selfing and facultative outcrossing. Pollen tube growth is relatively slow in *M. excelsa*, compared to other angiosperms. Due to the slow growth rate and relatively long styles, it takes between 10 to 15 days before the ovary is reached by the pollen (Schmidt-Adam et al. 1999).

Seed production

All ovules within the ovaries appear to be potentially fertile, as they have similar morphology and all contain an embryo sac. However the number of ovules that develop to form fertile seeds is very low, and this appears to be irrespective of pollen availability. It has been reported that seed production in natural environments is less than 10% (Wotherspoon 1993). Low fertility is common in the genus *Metrosideros*; for example the Hawaiian species *M. polymorpha* is thought to have a seed production rate of 8.9%–15% (Drake, as cited in Schmidt-Adam et al. 1999). Despite the low levels of seed production per capsule, the overall seed production per tree is still very high and sufficient to ensure the survival of the species. The reproductive strategy of *M. excelsa* is described as "wasteful but sufficient" (Schmidt-Adam et al. 2000). Once an ovule is successfully fertilised, a seed will develop, this matures into a small, oblong capsule. Capsules dry out and split open in March-April, releasing the tiny brown seed (Bergin & Hosking 2006). Wind is the main dispersal mechanism, carrying the seeds large distances, and providing a mechanism for gene flow between populations (Broadhurst et al. 2008).

Inbreeding and out breeding

The floral biology of *M. excelsa* presents a paradox, the large floral display attracts pollinators and supports out-breeding and cross pollination, however, the mass flowering episodes also mean there is a high probability that self-fertilisation will occur (Schmidt-Adam et al. 1999). The large floral structure of *M. excelsa* flowers coupled with the hermaphroditic phase allow cross and self-pollination as there is an absence of any evolutionary traits to avoid pollen and stigma interference (Schmidt-Adam et al. 1999). The large floral displays of *M. excelsa* are consistent with high levels of both autogamous and geitonogamous self-fertilisation. Both nectar and pollen are produced and offered as a reward to pollinators. It is possible for pollinators to distribute pollen on a stigma from the same flower or a stigma from a different flower, on the same tree (geitonogamy) and this may be the dominant type of fertilisation.

Autogamous pollination, whereby pollen moves to the female part of the flower without pollinator aid, is also possible. Because the stigma is protruding, it is only separated from the stamens by a few millimetres; this might be enough to prevent

some pollinator unaided fertilisation (Schmidt-Adam et al. 1999). However, this distance of separation is small in comparison to pollinator size, thus non precise moments from pollinators maybe sufficient to cause self-pollination. Controlled pollination experiments indicate that individual *M. excelsa* trees differ in their ability to set seed after self-fertilisation, thus natural populations are likely to be composed of a mosaic of self-compatible and incompatible individuals (Schmidt-Adam et al. 1999).

Inbreeding depression is late acting in selfing individuals of *M. excelsa*, as pollen tube growth, ovule/seed development and germination is not affected (Schmidt-Adam et al. 1999; Schmidt-Adam et al. 2000). However, Schmidt-Adam et al. (2000) found that after six months of seedling growth, inbreed individuals had markedly lower rates of shoot growth (Figure 6.6). It is probable that late acting inbreeding depression is associated with small effects at many gene loci rather than major effects at few gene loci. Natural selection may ultimately eliminate inbred individuals before they reach reproductive maturity (Schmidt-Adam et al. 2000).

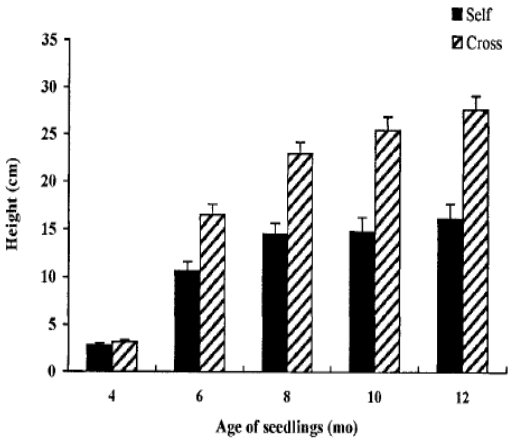

Figure 6.6: Height of *Metrosideros excelsa* seedlings after a 12 month growth period. Number of self-pollinated seedlings =56 and cross pollinated seedlings =50 (Taken from Schmidt & Adam et al. 2000)

6.11 Seed biology

Following mass flowering, *M. excelsa* produces thousands of tiny wind dispersed seeds. Seed has very low fertility rates and the majority of seed produced is sterile (Dawson 1968). While only a small portion of the seed produced will germinate, once an individual is established it can live for hundreds of years; a wasteful but effective strategy (Schmidt-Adam et al. 2002; Bergin and Hosking 2006). Mature seed capsules contain a mixture of filled (embryo-containing) and unfilled (embryo-lacking) seeds. Filled/fertile seeds are randomly distributed across the placenta, showing no obvious preferential position. *Metrosideros excelsa*, like most species within the genus, also have a low seed: ovule ratio. *Metrosideros excelsa* seeds lack endosperm tissue and have a thin two layered seed coat, making them extremely vulnerable to desiccation. Consequently, *M. excelsa* seed

can only persist in the soil for a short period and must germinate soon after dispersal (Schmidt-Adam et al. 2002).

6.12 Germination and establishment

The most significant event in the life cycle of a *M. excelsa* tree is seedling germination and establishment (Simpson 2005). Seedlings of *M. excelsa* are extremely small; each of the two seed-leaves/cotyledons is between 1–2 mm in length. *Metrosideros excelsa* have a germination strategy tuned-in to harsh and suboptimal environments. Germination is quick; initially biomass is allocated to the emerging root, which seeks out soil and rock fissures. Roots are covered in tiny hairs which cling to moist surfaces. Cotyledons and the first emerging leaves have a thick waxy cuticle which protects against desiccation. Further adventitious roots are formed at the stem base and after a season of growth young plants are usually a cluster of roots and shoots (Simpson 2005).

Figure 6.7*:* *Metrosideros excelsa* seedlings established on rocks, Matata Scenic Reserve, Bay of Plenty 2011.

6.13 Pollinator relationships

Metrosideros excelsa has previously been classified as ornithophilous, having characteristics which attract bird visitors, such as red coloration and copious nectar production. *Metrosideros excelsa* flowers also lack a strong scent (Godly 1979). Available flower pollinators in New Zealand include birds (7 spp.), bats (1 sp.), butterflies (16 spp.), and solitary bees (c. 40 spp.) as well as moths, beetles, and flies and several introduced bees (Godley 1979). *Metrosideros excelsa* is a generalist, thus does not rely on a single pollinator relationship. Known flower visitors include, but are probably not limited to the native honeyeaters (Meliphagidae), a range of introduced birds, native and introduced bees, as well as native geckos and bats (Schmidt-Adam et al. 2009).

There has been a dramatic shift in pollinators since the time of European settlement, and this has accompanied the decline in *M. excelsa* populations. The native honey eaters, which include the tui (*Prosthemadera novaeseelandiae*), the bellbird (*Anthornis melanura*) and the stitchbird (*Notiomystis cincta*) were once widespread, but now many are locally extinct; the stitchbird is restricted to Little Barrier Island, where the only self-sustaining population exists (DOC 2005). The original suite of pollinators has been largely replaced by exotic pollinators, such as non-native birds and honey bees that were introduced during the 1980s. These effects are most notable on the mainland, as native fauna populations on offshore islands are more isolated from introductions. A study by Schmidt-Adam et al. (2000) investigated the effects of this pollination shift on the reproductive system of *M. excelsa*; comparing outcrossing and self-pollination rates in island and mainland populations. The study revealed that outcrossing rates were among the lowest in the genus, however due to the ability of *M. excelsa* to use a wide range of pollinators, the reproductive system is largely resistant to shifts in local pollinators. Therefore the mainland populations do not suffer from enhanced inbreeding due to the prevalence of exotic pollinators (Schmidt-Adam et al. 2000).

A further study by Schmidt-Adam et al. (2009) has shown that native birds are more important pollinators of *M. excelsa* than native bees. This is likely to be due to a greater abundance of birds, larger body size and different foraging patterns, which make them more efficient at pollinating flowers and inducing seed set. The study also showed that birds promote outcrossing in the species, due to their high rate of inter tree movement. Honey bees were more efficient pollinators than native solitary bees; native bees made contact with the stigma in less than 10% of visits, while the larger honey-bees were six times more efficient.

Although birds and bees are among the most frequent visitors of *M. excelsa*, nocturnal visitation by New Zealand's endemic geckos and short-tailed bat (*Mystacina tuberulata*) have also been reported. The feeding habits of the short-tailed bat where not understood until an accessible population was studied in North Auckland (Godley 1979). It was found that the bats have an omnivorous diet, and feed on insects, fruit and nectar. The short tailed bat has a long tapering tongue, 1–1.2 mm wide; this is equipped with many fine hairs; an adaptation to nectar feeding which the endemic long-tailed bat, a sole insect feeder does not

have (Daniel 1976). *Metrosideros* and specifically *M. excelsa* pollen has been found in the droppings and stomach content of short-tailed bats (Daniel 1976; Arkins et al. 1999). On Little Barrier Island, short-tailed bats have significantly higher activity levels (indicated by echolocation calls) in the vicinity of flowering *M. excelsa* trees, compared to non-flowering trees (Arkins et al. 1999).

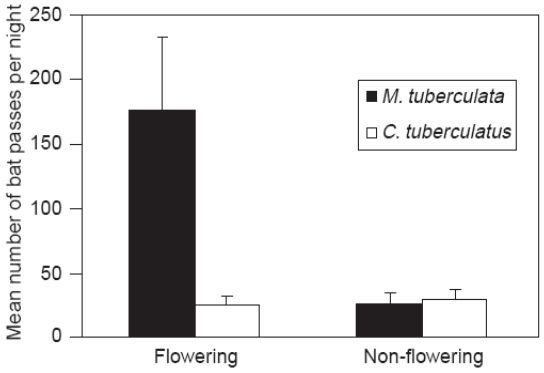

Figure 6.8: Bat activity associated with flowering and non-flowering *Metrosideros excelsa* trees on Little Barrier Island (taken from Arkins et al. 1999).

6.14 Changes during ontogeny

Metrosideros excelsa shows a smooth transition from juvenile to mature phenology, typical of homoblastic behaviour (Clements et al. 1999). The vegetative phase change is characterised by a transition from smooth glaborous juvenile foliage to adult leaves that possess a dense pubescence on the abaxial leaf surface (Kubien et al. 2007). Examination of anatomical and physiological characteristics that accompany this phase change has shown a constant ratio of intercellular to ambient CO_2 (constant $\delta^{13}C$). Rates of photosynthesis decreased in adult leaves, this may be due to a reduction in resources allocated towards carbon gain (Kubien et al. 2007). Also, as the degree of leaf pubescence increases, the degree that the stomata limited CO_2 uptake decreases; indicating that the control of water loss shifts from a physiological to a physical basis. This is likely to be associated with allocation of leaf resources away from photosynthesis. Kubien et al. (2007) suggest the dense pubescence of adult leaves may also play a role in biotic interactions, such as protecting against insect attack or fungal pathogens. The development of leaf pubescence was accompanied by anatomical changes. Adult leaves have an increased palisade and mesophyll depth, attributed to increased cell size as opposed to an increase in cell layers. Such a change may reduce light penetration and prevent sun damage of mature leaves. Nitrogen levels were found to be much higher in juvenile leaves, indicating a reallocation

of nitrogen in adult plants to areas where it is used for plant functions such as defence and reproduction rather than photosynthesis (Kubien et al. 2007).

The minimum light requirements *M. excelsa* juveniles may also increase as juveniles develop; a study which quantified the light environments occupied *M. excelsa* juveniles' found light environments significantly decreased with increasing juvenile height (Bylsma 2012: Chapter Four). However, this may not indicate an increased tolerance to shade as *M. excelsa* juveniles develop, but alternatively may be the result of juveniles being over-topped by faster growing species. Single mature *M. excelsa* trees are commonly observed growing beneath a closed canopy of taller species. It is likely these specimens preceded current vegetation, and were over topped by faster growing trees (Atkinson 1994).

6.15 Associated fungi

There is a total of 209 species of fungi known to be associated with indigenous *Metrosideros* species in New Zealand (McKenzie et al. 1999; Taylor et al. 2007). Very few of these are considered primary pathogens; however it is believed secondary pathogens, such as wood-rotting basidiomycetes may play a role in *Metrosideros* species die back following severe possum browse (McKenzie et al. 1999). The majority of fungi identified on *M. excelsa* are saprobes, which derive their nutrition from non-living plant material. *Leptomelanconium* sp. is a common and widespread saprobe found on *M. excelsa* foliage and it has the tendency to cause leaf spots and discolouration. Levels of infection can be very high on individual trees, however the fungi's effect on overall tree health is unknown. Payton (1998) made the observation that increased dieback in Westland rata (*Metrosideros umbellate*) and kamahi (*Weinmannia racemosa*) following the removal of the brush-tailed possum (*Trichosurus vulpecula*) populations, may in part, be attributed to fungal disease. It is suggested that damaged and stressed trees may allow fungi, which would otherwise be benign, to become serious pathogens (McKenzie et al. 1999). Changes in fungal population's pathogenicity after possum damage, has yet to be investigated in *M. excelsa*.

Metrosideros excelsa lack any ectomycorrhiza associations, however 19 endomycorrhiza have been identified to be associated with the inner tissues of *M. excelsa* roots. Experiments have shown that seedlings are very rapidly colonised

by the fungi and such fungi benefit the seedlings by increasing seedlings tolerance to environmental stresses (e.g. drought and low nutrient availability) and increasing seedlings relative growth rates; particularly when growing in infertile substrates (Simpson 2005).

6.16 History and early utilisation

Traditional use by Māori

Metrosideros excelsa is considered a medicinal plant by Māori. An infusion made from the inner bark was often used as a remedy for diarrhoea and dysentery (Brooker et al. 1961). The tohunga (chief priest) would make this sacred infusion by immersing the trees inner bark in water; the bark is then removed from the water after a short time, and the liquid ingested by the ill patient (Riley 1994). The bark of *M. excelsa* contains ellagic acid, and this has been shown to have antioxidant properties (Seeram et al. 2005); often used as an astringent in the treatment of diarrhoea and dysentery (Brooker et al. 1961). The inner bark of *M. excelsa* was also bound to gunshot and battle wounds, to soothe and treat for inflammation and help stop bleeding (Riley 1994). The inner bark was also chewed by Māori to alleviate tooth ache (Bergin & Hosking 2006).

The sweet nectar from the *M. excelsa* flowers also had medicinal values to Māori. The nectar was collected in large quantities by removing the flowers from the tree and tapping them against the inside of a calabash. Once a sufficient amount of nectar was attained, it was sucked through a hollow reed, to cure a sore throat (Riley 1994). Flowers of *M. excelsa* contain gallic acid, which is mildly antiseptic (Clarke 2007).

Early Māori used the hard wood of *M. excelsa* to make implements such as paddles, weapons and mauls. The high wood density meant it was also perfect for flax softening bats and pounders used to prepare bracken rhizomes for consumption (Bergin & Hosking 2006). Māori frequently used *M. excelsa* timber for boat building (Bergin & Hosking 2006) and in the final fitting-out stage of canoe building; the strong, curved thwarts of *M. excelsa* were commonly used to brace and strengthen the long narrow vessels (Clarke 2007). It is thought the hardness of the timber limited the woods use by Māori (Simpson 2005).

Traditional use by Europeans

Early Europeans were able to prepare *M. excelsa* timber much more easily than Māori, due to their advanced tools, and were limited only by the excessive weight of large pieces (Simpson 2005). Like Māori, early Europeans also used *M. excelsa* for boat building; the wood was extremely popular for this purpose in the upper North Island. The reason for its popularity was due to its resistance to the tunnelling teredo worm, a bivalve mollusc (Simpson 2005). Thomas Kirk, an early botanist from England, considered *M. excelsa* wood to be second only to *Vitex lucens* in its resistance to the tunnelling worm (Bergin & Hosking 2006). However, the coastal habit of *M. excelsa* further encouraged its use, as *Vitex lucens* predominantly grew inland and accessing the timber was therefore more difficult (Simpson 2005).

Before glues became readily available, *M. excelsa* was often used in pleasure craft and work boats which required very strong hulls with many knees. The natural shapes of *M. excelsa* roots and branches were perfect for this (Simpson 2005). Consequently, *M. excelsa* forests were greatly reduced in areas surrounding boat building yards, and this decline continued well into the 1940's (Bergin & Hosking 2006).

Metrosideros excelsa timber was also traditionally used for making fence posts and burnt as firewood (although difficult to split). Because the flowering period of *M. excelsa* coincides with Christmas, early European settlers also used the flowers as a substitute for holly, thus the species earned the name 'New Zealand's Christmas tree" (Conly & Conly 1988; Simpson 2005; Bergin & Hosking 2006).

6.17 Ecology and ecological preferences

Metrosideros excelsa can be described as an ecological opportunist. Trees flower profusely in summer, and by autumn, have produced thousands of tiny seeds. These seeds can then be dispersed several hundred kilometres by the wind; maximising the seed spread to ideal conditions; a wasteful but effective enough strategy to ensure the species' survival (Schmidt-Adam et al. 2000). Once established, *M. excelsa* are extremely long lived, with individual trees reaching 1000 years or more (Bylsma 2012: Chapter Four). Mature *M. excelsa* forests take

c. 250 years to develop (Clarkson & Clarkson 1994). Such longevity is not a common trait among pioneer species (Bergin & Hosking 2006).

An important ecological characteristic of *M. excelsa* is its ability to tolerate exposed hostile sites, and establish in a wide range of habitat types; including grassland and fern-land, on headlands, sand dunes, coastal rocky cliffs, volcanic bolder fields and ash deposits. These sites are generally sub-optimal and too hostile for most other woody, pioneering, species (Wardle 1991). *Metrosideros excelsa* is superbly adapted to the coastal cliffs of the North Island; the small seeds are often caught in crevices where pockets of soil exist. The roots spread along rock faces, and penetrate fissures, anchoring the tree and gaining access to limited soil resources. Aerial roots which reach the ground add to the stability of the tree (Wardle 1991). However, establishment of *M. excelsa* is limited by frost exposure. Adult trees can survive temperatures as low as -3˚C with little to no leaf damage (Sakai & Wardle 1978), however seedlings are less tolerant. Low temperature regimes have been shown to reduce the overall germination and slow the rate of germination and seedling development (Wotherspoon 1993). Thus *M. excelsa* thrive on the northern coastline, where there is a mild temperate climate and sufficient rainfall (Simpson 2005). Although the species is described as drought tolerant, they are seldom found growing in regions with an annual rainfall less than 1000 mm (Simpson 2005).

Metrosideros excelsa seedlings are shade intolerant (Bergin & Hosking 2006). The small wind dispersed seeds of *M. excelsa* carry very few food or energy reserves, so germination is generally restricted to open sites where *M. excelsa* do not have to compete with, or grow up through other vegetation (Wotherspoon 1993). The light environment occupancy has been assessed for *M. excelsa* juveniles and suggests the minimum light requirements of juveniles is 3.68% of canopy openness, however juveniles more frequently occupy sites with between 16–32% canopy openness (Bylsma 2012: Chapter Four). However, single mature *M. excelsa* trees have been observed growing beneath a closed canopy of taller species. It is likely these specimens preceded current vegetation, and were over topped by faster growing trees; often evidenced by multiple trunks and stems (Atkinson 1994). *Metrosideros excelsa* trees are extremely tolerant of gusty and salt laden winds. On very exposed sites the generally well rounded canopy of a

M. excelsa can become shaped and moulded to the hillsides by the strong winds (Wardle 1991).

Soil and substrate strongly influence the distribution of *M. excelsa*. The species' preference for fertile, hard rocky substrates means it becomes less common in areas where the predominant substrate is soft mud or sandstone. Such substrates are also unstable as they lack fissures for *M. excelsa* roots to penetrate and anchor the trees. An exception to this is the population that exists on a 1–2 km coastal mudstone cliff, near the Paparoa reef, Taranaki. *Metrosideros excelsa* here have become an integrated part of the erosion cycle. *Metrosideros excelsa* has a strong affiliation for volcanic substrates and naturally grows in close proximity to thermal activity (Clarkson & Clarkson 1994); on Whale Island, in the Bay of Plenty, stunted *M. excelsa* shrubs grow within metres of steaming springs and fumaroles (pers. obs).

6.18 Associated plant species

Comparison of *M. excelsa* forest, with other more widespread forest types in New Zealand, highlights the unique and varied mix of flora in *M. excelsa* forest, and the generally low species richness. Many *M. excelsa* stands, particularly those on exposed seaward facing sites have a depauperate flora; coastal forest surveyed in the Bay of Plenty often had <15 vascular species per 400 m^2 (Bylsma 2012: Chapter Three). In part, the low species richness observed in *Metrosideros* forest reflects the habitat severity, but also the tendency of the *Metrosideros* to retard the rate of which a diverse community can develop (Atkinson 2004). *Metrosideros excelsa* can however, form tall coastal forest with c. 20 m canopies also containing a mixture of coastal and lowland species (Table 6.1) such as *Beilschmiedia tarairi*, *Beilschmiedia tawa*, *Corynocarpus laevigatus*, *Dysoxylum spectabile*, *Kunzea ericoides*, *Litsea calicaris* and *Vitex lucens* (Bergin & Hosking 2006; Bylsma 2012: Chapter Three). Understories in this tall forest commonly include *Brachyglottis repanda*, *Coprosma* spp., *Geniostoma rupestre*, *Hedycarya aborea*, *Melicytus ramiflorus*, *Pseudopanax lessonii* and *Pseudopanax arboreus*. The forest floor generally has a dense covering of *M. excelsa* litter and seedlings can be scarce, however the ferns *Adiantium cunninghamii*, *Asplenium oblongifolium*, *Asplenium polyodon*, *Microsorum pustulatum* and *Doodia*

australis are common, as are the monocots *Astelia banksii* and *Machaerina sinclairii* (Bylsma 2012: Chapter Three).

On estuary and harbour margins, *M. excelsa* merges with mangroves on the inter-tidal mudflats. Where it grows on the Rotorua Lakes margins it is associated with a diverse range of low-land broadleaved species, specifically *Knightia excelsa* and *Beilschmiedia tawa*. *Metrosideros excelsa* is also associated with *Nothofagus truncata*; in areas of the Raukumara Ranges *Nothofagus truncata* descends down from the ridges and forms mixed stands with *M. excelsa* in the valleys (Wardle 1991). This association is also found in the Bay of Plenty Region, most obviously in the Matata Scenic Reserve, and also smaller fragments in the Ohiwa Harbour area (RJ Bylsma unpubl. data). *Rhopalostylis sapida* assemblages are also common in damp regions of mature *Metrosideros* forest (Hamilton & Atkinson 1961; Bylsma 2012: Chapter Three).

Epiphyte species are generally not abundant in *M. excelsa* forest (Bylsma 2012: Chapter Three), probably due to low humidity and high exposure. However, in sheltered or mature forest epiphytes become more common, inhabiting the forks of *M. excelsa* branches (Figure 6.9d). In a survey of *M. excelsa* forests in the Bay of Plenty, common epiphytic species included *Pyrrosia eleagnifolia, Asplenium flaccidum, Microsorum scandens*, *Microsorum pustulatum*, *Blechnum filiforme*, *Astelia solandri* and *Collospermum hastatum*. Climbers and lianas were less common and included *Clematis foetida*, *Clematis paniculata* and *Ripogonum scandens* (Bylsma 2012: Chapter Three).

A survey of vegetation communities on Rangitoto Island showed that vegetation patches dominated by *M. excelsa* frequently supported epiphytic species such as *Hymenophyllum* spp., *Microsorum pustulatum*, *Pyrrosia eleagnifolia*, *Asplenium oblongifolium*, *Brachyglottis kirkii*, *Trichomanes reniforme*, *Asplenium flabellifolium* and *Ctenopteris heterophylla* (BD Clarkson, University of Waikato, unpubl. data; Bryan et al. 2011). Prior to the Tarawera eruption (1886), Kirk (1872) reported *M. excelsa* trees growing on the shores of Lake Tarawera to be rich with epiphytic species including the shrub epiphytes *Griselinia lucida* and *Pittosporum cornifolium*, as well as *Astelia solandri* (Bryan et al. 2011).

Figure 6.9: (a) *Metrosideros excelsa* forest, Mayor Island. **(b)** *Rhopalostylis sapida* assembledege, Ohope Scenic Reserve. **(c)** *Metrosideros excelsa* forest merging with mangroves on the inter-tidal mud flat, Ohiwa Harbour. **(d)** Large *Metrosideros excelsa* tree hosting an array of epiphytic species, Orokawa Reserve, Waihi Beach.

Table 6.1: Recorded vegetation types with *Metrosideros excelsa* as a dominant component.

Vegetation Type	location	Author
Metrosideros/ Pseudopanax lessonii forest	Bay of Plenty	Beadel & Shaw 1988; RJ Bylsma Unpubl. Data
Metrosideros/ Melicytus ramiflorus - Pseudopanax lessonii forest	Bay of Plenty	RJ Bylsma Unpubl. Data
Metrosideros/ Myrsine australis - Myrsine ramiflorus forest	Bay of Plenty	RJ Bylsma Unpubl. Data
Metrosideros/ Myrsine australis - Coprosma macrocarpa - Coprosma lucida forest	Bay of Plenty	RJ Bylsma Unpubl. Data
Metrosideros/ Melicytus ramiflorus - Cordyline australis forest	Bay of Plenty	RJ Bylsma Unpubl. Data
(*Kunzea*) *Metrosideros/ Pseudopanax arboreus - Pseudopanax lessonii* forest	Bay of Plenty	RJ Bylsma Unpubl. Data
(*Knightia*) *Metrosideros/ Myrsine australis- Melicytus ramiflorus* forest	Bay of Plenty	RJ Bylsma Unpubl. Data
Metrosideros/ Coprosma macrocarpa - Cyathea dealbata - Myrsine australis forest	Bay of Plenty	RJ Bylsma Unpubl. Data
Metrosideros/ Dysoxylum- Beilschmiedia- Cyathea dealbata forest	Bay of Plenty	RJ Bylsma Unpubl. Data
(*Cortaderia jubata*) *Coriaria arborea/ Metrosideros - Coprosma robusta* scrub	Bay of Plenty	RJ Bylsma Unpubl. Data
Metrosideros forest	East Coast North Is.	Regnier et al. 1988; Beadel & Shaw 1988
Metrosideros- (*Beilschmiedia tawa*) - broadleaf forest	East Coast North Is.	Regnier et al. 1989
Metrosideros - Vitex lucens forest.	East Coast North Is.	Regnier et al. 1990
(*Metrosideros*) / *Kunzea ericoides* scrub	East Coast North Is.	Regnier et al. 1991
Metrosideros forest	Little Barrier Is.	Hamilton & Atkinson 1961
Metrosideros / broad - leaved forest	Little Barrier Is.	Hamilton & Atkinson 1962
Metrosideros - Litsea calicaris forest	Bay of Plenty	Beadel & Shaw 1988
Metrosideros rockland	Bay of Plenty	Beadel & Shaw 1988

6.19 Growth Rates

Metrosideros excelsa growth rates have been calculated from stem disks and from diameter growth in permanent quadrats in *M. excelsa* forest (Clarkson & Clarkson 1990; Bylsma 2012: Chapter Four). Stem disks were collected from Mayor Island, White Island and the Bay of Plenty mainland. The diameter age-relationship has been modelled form the combined stem disk data (*n*=31), illustrated in Figure 6.10. Initially stems had high growth rates, producing annual growth rings which exceeded 5 mm. Annual diameter growth rates subsequently decrease with increasing stem age; the models suggests stem growth rates begin to plateau after stems reach c. 200 years, when growth rates slow down to less than 2 mm year^{-1}. Pardy et al. (1992) assessed *Metrosideros* growth rates in planted stands and small groves, finding that the mean diameter growth rate was 9.7 mm year^{-1}; well above those calculated for natural stands. Similarly, Bergin and Hosking (2006) reported *Metrosideros* diameter growth rates for individually planted trees (>100 years ago) in areas outside the species natural range. Growth rates ranged from 0.9–1.8 mm year^{-1}, also higher than those calculated from stem disks. Plantation sites are likely to be less hospitable and subject to less exposure than the natural stands and this may explain growth rate differences.

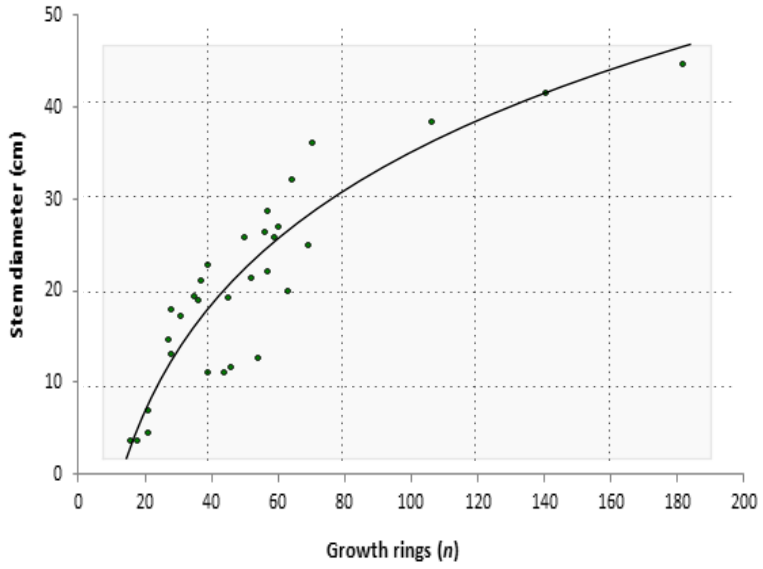

Figure 6.10: Gompertz model of stem diameter (cm) and age relationship, for Metrosideros excelsa stem disks, Mayor Island (*n*=5), White Island (*n*=10), Bay of Plenty mainland (*n*=16) (Bylsma 2012: Chapter Four).

6.20 *Metrosideros excelsa* forest dynamics

Metrosideros excelsa characteristically establishes on primary surfaces of open sites (Clarkson & Clarkson 1990). Following colonisation, it is expected to take c. 250 for mature forest to develop (Carkson & Clarkson 1990; Bylsma 2012: Chapter Four). In the Bay of Plenty, stands which exceed 300 years have larger canopy contributions of mid and late successional tree species. *Metrosideros excelsa* establishment generally gives rise to high density pure stands without further *M. excelsa* recruitment. As a result, stands generally have cohort populations and these subsequently undergo a large degree of self-thinning. A sequence of forest development, from young developing stands (c. 35 years) through to mature forest (> 300 years) has been quantified for a number of stands in the Bay of Plenty Region, illustrated on Figure 6.11, and shows a decline in *M. excelsa* stems density from >2000 to <400 stems ha^{-1} over a development period of c. 300 years. This decline in stem density was coupled with an increase in basal area from <20 m^2 ha^{-1} to an average of 50 m^2 ha^{-1} in the first 70 years of forest development, basal area did not noticeably increase thereafter (Bylsma 2012: Chapter Three). Self-thinning of *Metrosideros* stems is more prevalent in early phases of forest development; however this has little effect on total *Metrosideros* canopy foliage, as gaps are successively filled by surviving stems. Self-thinning in mature forests does result in a decrease of *Metrosideros* foliage; allowing later successional species to penetrate the canopy.

As forest develops, canopy height also increases, typically from > 2 m in scrub, to approximately 14 m in young forest (c. 30 years), and eventually to 20 m in mature forest. This relationship however, is confounded by forest location; gully sites generally have higher canopies than ridge sites and forest exposed to the sea always have a lower canopy than equivalent aged inland sites (Bylsma 2012: Chapter Three).

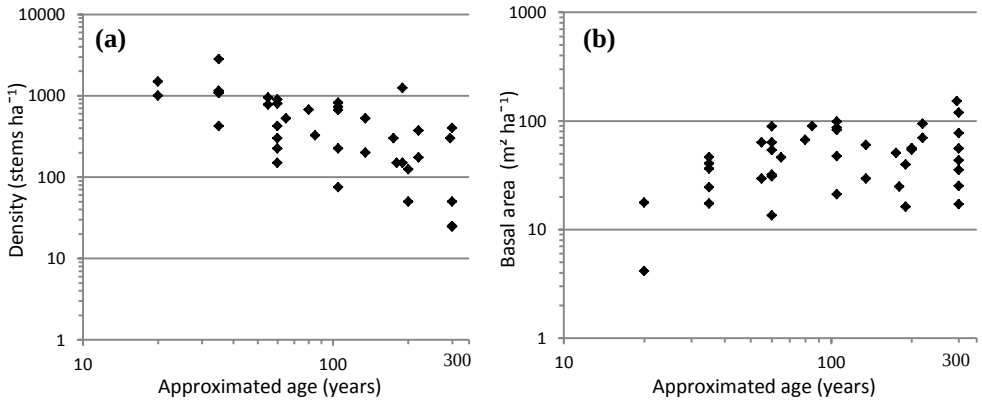

Figure 6.11: (a) Density versus approximated age of *Metrosideros excelsa* stands in in 39 quadrats, including re-measurement data from four permanent quadrats. **(b)** Basal area versus approximated age of *Metrosideros excelsa* stands in in 39 quadrats, including re-measurement data from four permanent quadrats. All axis are log scales (Bylsma 2012: Chapter Four).

6.21 *Metrosideros excelsa* forest succession

Metrosideros excelsa is an early colonist and once established on the landscape undoubtedly alters the physical environment; creating leaf litter, organic matter build up, shade and humidity, which ultimately facilitates the arrival and establishment of later successional, shade tolerant species. On Rangitoto Island, lava flows and cone building tephra eruptions have created 20 km^2 of sterile substrate (primarily basaltic *aa* lava) for species colonisation (Clarkson 1990). *Metrosideros excelsa* is one of the first woody species to colonise and establish, preceded only by lichens, mosses and algae. *Metrosideros excelsa* effect the environment here; the spreading canopy reduces ground temperatures below, and increases humidity. Beneath the canopy, fallen leaf litter decays to form humus, which in turn stores water. *Metrosideros excelsa* trees also attract birds, which bring in seed and nutrients (Bergin & Hosking 2006). As a result, the drip zones beneath *M. excelsa* become centres for further community development and in places, these centres have coalesced, giving rise to a continuous canopy (Clarkson 1990). Emergent *Knightia excelsa* are the first to penetrate the dense *M. excelsa* canopy on the older flows, and these are indicative of early forest development (Clarkson 1990).

In contrast to other early colonising tree species, such as *Kunzea ericoides* and *Leptospermum scoparium, M. excelsa* retains its dominance on the landscape for a much longer time period (125 cf. 250 years) and can retard the rate of which a

diverse community could develop (Atkinson 2004; Bylsma 2012: Chapter Four). Primarily this is achieved by: the species dense shading canopy which is difficult for other species to penetrate; slowly decomposing leaf litter which inhibits seedling germination; and the species longevity which allows *M. excelsa* to persist on the landscape for centuries (Atkinson 2004; Bergin & Hosking 2006). These competitive traits also inhibit regeneration of *M. excelsa*, thus stands generally have cohort populations (Clarkson & Clarkson 1994; Bylsma 2012: Chapter Five).

Metrosideros excelsa is a species tuned-in to disturbance; on White Island (Bay of Plenty), unique conditions, including continuous volcanicity, extreme soil conditions and a depauperate flora, has led to the species regeneration beneath the disturbed *M. excelsa* canopy; attributed to the species ability to re-sprout from epichormic buds and recommence flowering soon after disturbance (Clarkson & Clarkson 1994). White Island has been volcanically active since 1826 and this has caused significant damage to the islands vegetation; reducing the extent of *M. excelsa* forest by more than 60%. Population structure (Figure 6.12) reported by Clarkson & Clarkson (1990), allude to the many disturbance events and disturbance severities which have shaped the islands vegetation; for example a single large stem in the 70 cm dbh size class in the Ohauora plot, suggests it is a relic of a much earlier colonising phase (Clarkson & Clarkson 1994).

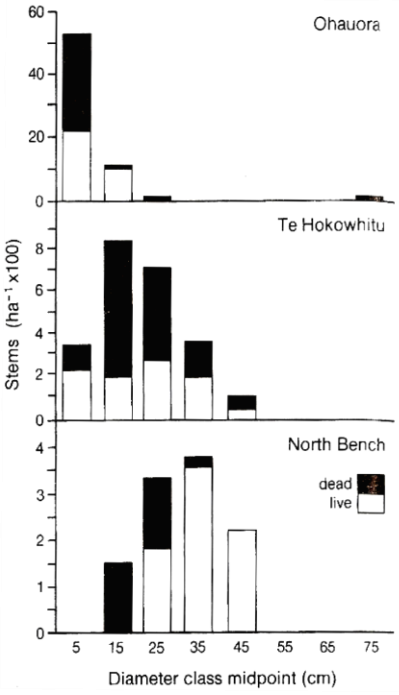

Figure 6.12: Size class structures of three White Island stands of *Metrosideros excelsa* (taken from Clarkson & Clarkson 1994).

Following seedling establishment, *M. excelsa* initially forms scrub or shrub-lands, which subsequently mature to even-aged stands without further *M. excelsa* recruitment. Other primary immigrants, which may form mixed stands with *M. excelsa* commonly include *Kunzea* and *Leptospermum*, however these species are less tolerant of coastal conditions, and have shorter life spans, thus may only persist in *Metrosideros* forest for c. 200 years, in semi-coastal and inland localities. On northern offshore islands, *M. excelsa* forest commonly forms

mosaics with *Kunzea* forest, rather than mixed stands (Atkinson 1994). On Whale Island (Moutohora), Bay of Plenty, *Cordyline australis* has also established in open sites, and formed mixed stands with young *M. excelsa* (Bylsma 2012: Chapter five). A suite of shrub and understory species commonly establish within young forest (>60 years old), species include *Coprosma repens, Coprosma robusta, Pseudopanax lessonii, Geniostoma rupestre, Myrsine australis* and *Melicytus ramiflorus*.

Two studies have examined the sequence of *M. excelsa* forest succession and show in the absence of disturbance, predominantly shade tolerant, bird disperesed species, eventually replace *M. excelsa* and early colonists (Atkinson 1994; Bylsma 2012: Chapter Three). Following 60–180 years of forest development a suite of mid-successional, shade tolerant tree species arrive and establish, including *Cornyocarpus laevigatus*, *Vitex lucens* and *Dysoxylum spectabile*. The next stage of forest succession involves the arrival of *Beilschmiedia tarairi* and/or *Beilschmiedia tawa*. In favourable locations (such as Hen and Chicken Island) these species can replace *M. excelsa* in the canopy after 200 years (Atkinson 2004). In the Bay of Plenty however, *Beilschmiedia tarairi* is not naturally common and *Beilschmiedia tawa* dominated forest is expected to replace *M. excelsa* following a minimum developing period of 300 years (Figure 6.13). Mid-successional species also contribute, however to a lesser degree than *Beilschmiedia*, as mid-successional species may be reliant on canopy gap formation to initiate height growth (Smale & Kimberley 1983; Bylsma 2012: Chapter Four).

In areas prone to frequent disturbance, such as on steep, exposed, rocky coastal headlands, *Metrosideros* forest is likely to have a cyclic succession, as no other species are as capable of survival in such localities. Cyclic *Metrosideros* succession is particularly evident in a small forest stand, which inhabit a 1–2 km coastal cliff, near the Paparoa reef, Taranaki. *Metrosideros* here have become an integrated part of the erosion cycle and no trees are older than c. 300 years due frequent erosion. The sea cuts into the cliffs, forming caves. Caves eventually collapse, along with the above strata and *M. excelsa* forest. Following this, erosion via rain, wind and gravity works to smooth out the rubble and re-stabilise the cliff, which is then re-vegetated by *M. excelsa*. Generally regeneration occurs on the inner slopes, however continuous erosion by the sea results in the stand being

positioned back on the headland, where the cycle continues (Simpson 1997; Simpson 2005).

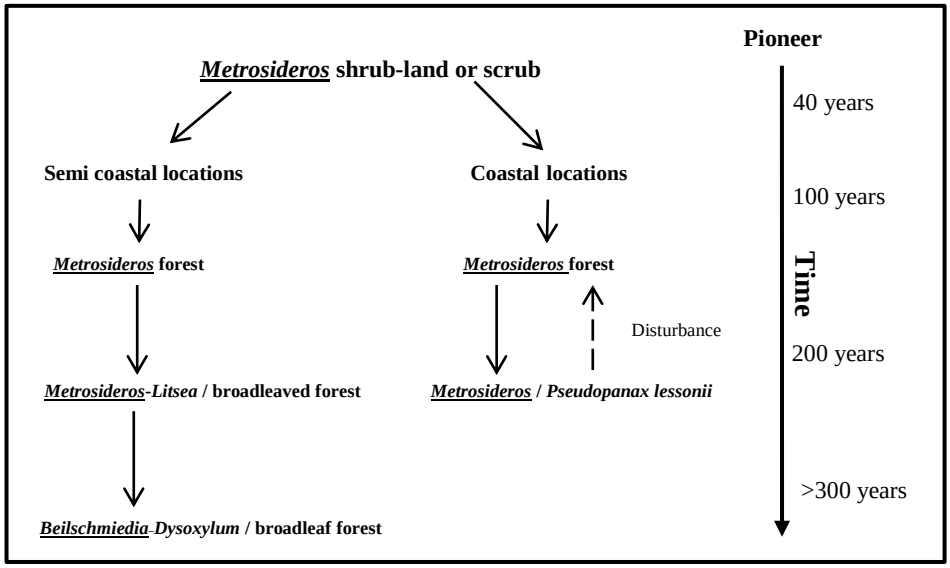

Figure 6.13: Schematic summary of *Metrosideros* forest succession in relation to time, for forest in the Bay of Plenty Region. Note time scale is approximate. (Bylsma 2012: Chapter Five)

6.22 Conservation

In the past, the greatest threat to *M. excelsa* forests has been land clearance by fire, followed by tree felling for the ship building industry (Young et al. 2001). For many years this destruction to *M. excelsa* forests went unnoticed, due to the common distribution of the species in cities, streets and frequently visited beaches; thus the species appeared to be abundant, even though the occurrence of intact natural *M. excelsa* ecosystems was drastically declining (Simpson 2005). By 1989 it was believed 90% of the original area of *M. excelsa* was lost (Hosking 2000), this figure rose to nearly 100% in the west, where refuges on steep cliffs and bluffs were few and infrequent. As a result *M. excelsa* was considered a candidate for the threatened plant list (de Lange et al. 1999). Remaining *M. excelsa* forest on the mainland is largely reduced to isolated stands, and individual trees (Young et al. 2001); thus *M. excelsa* forest is an ecosystem which most people will never have the opportunity to see (Simpson 1994).

The Project Crimson Trust manages a sponsorship programme that arose in response to the vulnerable state of *M. excelsa* forests that was identified in a 1998 species health assessment (Hosking 2000), which also indicated that remaining trees were threatened by possum browsing, fire and stock damage, and a lack of

regeneration. The trust is a community focussed project dedicated to the protection and enhancement of New Zealand's *M. excelsa* population. Over the years, it has involved many schools, organisations and community groups; raising the awareness of *M. excelsa* and undertaking hundreds of community based projects. A re-assessment of the health of *M. excelsa* forests, ten years after the Project Crimson Trust was established, showed positive results (Hosking 2000); regeneration sites had increased, possum damage had decreased, fencing around stands had increased, and therefore stock damage decreased.

Hosking & Simpson (2011) describe the current status of *M. excelsa* as still declining. This is mostly the combined result of animal browsing, disease and the limited nature of natural regeneration. The decline of *M. excelsa* is particularly evident in areas where possums and stock are not controlled; whilst the species is able to withstand salt and wind damage, it succumbs easily to damage by browsing animals. The leaves of *M. excelsa* are highly palatable, and it only requires a few possums to substantially defoliate a tree. Following this, trees react by reducing flower production and creating many epicormic shoots to produce new canopy foliage which in turn alters the growth from of the tree (Hosking 2006).

In winter possums selectively browse old foliage, however in spring and summer it is the young leaves and vegetative buds which are targeted. As a consequence, possum ravaged trees are more intensively grazed because of the plentiful young buds. Once possums have removed c. 80% of a tree's foliage, death is inevitable (Wotherspoon 1993). Young trees however, may be saved if they are protected from further possum damage, for example using banding or possum control. It has been suggested the wider use of 1080 would undoubtedly benefit the long term health and prosperity of *M. excelsa* (Baigent-Mercer 2010). As well as being prone to possum damage, *M. excelsa* trees are also particularly sensitive to disease, and trampling by foot traffic and domestic stock; the latter is due to their surface spreading roots (Simpson 1994). Accidental and intentional fires are also a serious concern, particularly in recreational areas.

Re-establishment of *M. excelsa* through restoration plantings has been shown to have variable success and nursery raised seedlings have difficulty establishing (Bergin & Hosking 2000). The use of locally sourced material is important for

this species due to the high degree of genetic differentiation between populations and a complex geographic pattern, and where possible seed should be sourced from the larger populations as they have higher levels of genetic diversity (Broadhurst et al. 2008).

Many cultivars of *M. excelsa* are available; however, if these are introduced into native populations genetic pollution may occur, lowering the population's fitness in local conditions (Wotherspoon 1993). Atkinson (1994) suggests careful thought is required for the appropriate use of *M. excelsa* in restoration plantings. If the management goal is to increase biological diversity, the use of *M. excelsa* as primary cover may not be appropriate due to its ability to slow the rate at which a diverse community can develop.

Chapter Seven: Synthesis and recommendations

7.1 Discussion

This research has enhanced the understanding of *Metrosideros* forest ecology, provided new quantitative data determining the current composition and structure of *Metrosideros* forest in the Bay of Plenty and quantified a sequence of forest development. By installing a network of re-locatable quadrats this research has also provided a baseline for future research which will further enhance our understanding of forest succession. This new information will also aid *Metrosideros* forest management and conservation.

Metrosideros forests, particularly those on exposed seaward facing sites, have a depauperate flora. Many *Metrosideros* stands Bay of Plenty, contained <15 vascular species (per 400 m^2). In part, the low species richness observed in *Metrosideros* forest reflects the harsh and inhospitable sites the forest occupies, as well as the tendency of *Metrosideros* retard the rate at which a diverse community can develop. This is a likely result of the species densely shading canopy and slowly decomposing leaf litter, which creates sub-optimal germination conditions in young forest. However, forests became more diverse inland and in more sheltered localities; species richness in such locations are comparable to other indigenous forest types (i.e., *Nothofagus* forest or mixed *Nothofagus*-hardwood forest).

Ordination and classification of quadrat data delineated nine distinct forest types, each type with a distinct species composition, and this variation was partially be explained by geographic position, distance from the sea, topographic landform, as well as site age. Understories within young *Metrosideros* forest generally comprised a sparse shrub layer overtopped by a sub-canopy dominated by either tree ferns in steep inland localities, *Pseudopanax lessonii*, *Coprosma* spp. and *Melicytus* on coastal headlands, or *Coprosma* spp. and *Myrsine*, semi-coastal forest. Mature forest had significant contributions of mid and late successional species, such as *Beilschmiedia*, *Litsea* and *Dysoxylum*.

Diameter growth rates of *Metrosideros* showed a strong relationship with tree age and mainland stems had significantly higher diameter growth rates than those

growing on the islands Tuhua and Whakaari. Slower growth rates of Whakaari stems was expected due to continuous volcanic activity on the island. *Metrosideros* stem initially had high diameter growth rates; on the mainland these often exceeded 4 mm year^{-1} in the first 80 years of development. However, diameter growth rates subsequently decreased as stems matured, to less than 2 mm year^{-1}. Surveyed *Metrosideros* vegetation ranged from c. 6–>300 years old; thus a complete sequence of forest development was quantified, from young establishing scrub and building stands, through to advanced stages of mature forest. In the Bay of Plenty, mature *Metrosideros* forest could develop within c. 250 years, and stands which exceeded 300 years had significant canopy contributions from shade tolerant species, thus these stands represent a compositional shift away from *Metrosideros* dominated forest.

Throughout development, *Metrosideros* stem density continuously decreases due to self-thinning, and this is most prevalent in young forests (<60 years old). Self-thinning in young stands is characterised by the death of entire trees, however in older, more mature forest, self-thinning is characterised by the sequential loss of tree limbs, which eventually results in the demise of the tree. The loss of *Metrosideros* stems in young forest does reduce *Metrosideros* canopy foliage; as canopy gaps are subsequently filled by surviving *Metrosideros* stems. However, the loss of stems in more mature forest (>60 years), creates canopy gaps and these are instead filled by the shade tolerant species, which eventually succeed *Metrosideros*. The replacement strategies among key species involves establishment at different phases of forest development, and this directly reflects species' differing shade tolerances.

Following establishment, *Metrosideros* forms scrub or shrub-lands, which mature to form even-aged stands without further *Metrosideros* recruitment. Other primary immigrants, which may form mixed stands with *Metrosideros* include *Kunzea* and *Leptospermum*, however these species have shorter life spans, and may only persist in developing *Metrosideros* forest for c. 200 years. A suite of shrub and understory species commonly establish beneath young *Metrosideros* in young forest (>60 years old), species include *Coprosma repens*, *Coprosma robusta*, *Pseudopanax lessonii*, *Geniostoma rupestre*, *Myrsine australis* and *Melicytus ramiflorus*. The light environments occupied by juveniles of these species did not significantly differ from that of the randomly sampled forest understory. Mid and

late successional species were predominantly bird dispersed, shade toleraters; *Litsea*, *Dysoxylum*, *Beilschmiedia* and *Corynocarpus*. *Litsea Dysoxylum* and *Corynocarpus* commonly established following 60–180 years of forest development, whereas the establishment of *Beilschmiedia* predominantly occurred following 180 years of forest development. *Beilschmiedia* dominated forest is expected to replace *M. excelsa* following a minimum developing period of 300 years. Mid-successional species are also likely to contribute to forest composition, however to a lesser degree than *Beilschmiedia*, as mid-successional species may be reliant on canopy gap formation to initiate height growth whereas *Beilschmiedia* is capable of continuous regeneration in the absence of canopy disturbance.

The present research also contributes to the national reporting of quantitative data describing the structure and composition of New Zealand's indigenous forests. Previously, quantitative vegetation classification systems have focused on old-growth forest types and their potential distribution on the landscape. *Metrosideros* forest has a restricted distribution, and is considered a rare vegetation type. In part, this has contributed to *Metrosideros* forest being left out of previous national vegetation classification schemes. This research provides new quantitative data depicting the current composition and structure of *Metrosideros* in the Bay of Plenty and the network of quadrats implemented during this study will provide a baseline for further research. Furthermore, the first comprehensive quantitative model of succession in *Metrosideros* forest in the Bay of Plenty has been proposed; and this demonstrates linkages between species' differing shade tolerances, regenerative strategies and successional status.

7.2 Future research and recommendations

This research has installed a network of 33 re-locatable quadrats within *Metrosideros* dominated forest. It would be appropriate to re-measure at least a selection of these, as well as the four existing permanent quadrats used, at ten yearly intervals, to confirm or otherwise, the trends identified in this study. Permanent quadrats measured at appropriate intervals provide benchmarks, against which long-term ecosystem change can be assessed. In contrast, the chronosequence method used here to deduce successional trends involved surveying forest at different sites and at different stages of forest succession and

does not separate temporal from site effects. To eliminate site variability, long term monitoring of quadrats is required.

Interspecific shade tolerance variation was identified as a key determinant of the successional pathways within *Metrosideros* forest, however observations also suggest that soil development may be equally important, and has potential to affect seedling germination and establishment. Soil descriptions and analysis of soil components at each of the study sites, along with trials designed to assess key species germination and establishment requirements (with respect to soil, substrate and nutrients), may also aid the understanding of successional pathways within *Metrosideros* forest.

Metrosideros forest and scrub commonly dominated extremely steep, rocky and drought prone sites. The precarious nature of these sites meant the quadrat based method used was unsuitable. Development of a semi-quantitative method to determine species composition at such locations would be beneficial in identifying the complete range of vegetation types and associated species.

Although this study focussed only on *Metrosideros* forests in the Bay of Plenty Region, comparison with other the limited number of other studies suggests the results are applicable to *Metrosideros* forest elsewhere in the North Island. However, a more extensive survey, investigating the current state of *Metrosideros* forests throughout the species natural range would be beneficial.

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Appendices

Appendix one: Forest survey quadrats size, location and identifier. SR= Scenic Reserve. Sci R= Scientific Reserve.

Quadrat name/identifier	Reserve/location	Quadrat size (m)	GPS (corner subplot a)		
			Easting	Northing	±
Kohi1	Kohi Point SR	20 x 20	1953136	5792065	5
Kohi2	Kohi Point SR	20 x 20	1953138	5791988	5
Kohi3	Kohi Point SR	20 x 20	1953138	5791866	5
Kohi4	Kohi Point SR	20 x 20	1953054	5791935	-
Kohi5	Kohi Point SR	20 x 10	-	-	-
Oho1	Ohope SR	20 x 20	1954124	5790223	5
Oho2	Ohope SR	20 x 20	1954358	5790409	5
Oho3	Ohope SR	20 x 10	1953548	5789623	4
Oho4	Ohope sR	20 x 20	1954296	5790260	4
Oho5	Ohope SR	3 x 10 x 10	1954080	5789859	4
Oho6	Ohope SR	20 x 20	1954061	5790230	6
Matata slip	Matata SR	20 x 5	1930194	5799396	5
Mat1	Matata SR	20 x 20	1930263	5799393	4
Mat2	Matata SR	20 x 20	1930259	5799360	5
Mat3	Matata SR	20 x 20	1929234	5799994	10
Mat4	Matata SR	20 x 20	1930353	5799273	3
MatS	Matata SR	1 x 1	1929189	5800013	5
Mater1	Matata SR	5 x 10	1929255	5800052	6
Mater2	Matata SR	10 x 10	1929272	5800025	4
Mater3	Matata SR	5 x 10	1929238	5800027	5
Piko1	Pikowai 1	20 x 20	1926006	5801855	4
OscRev1	Oscar reeves SR	20 x 20	1966212	5785529	6
OscRev2	Oscar reeves SR	20 x 20	1966196	5785445	7
Oro1	Orokawa SR	20 x 20	1859828	5857323	4
Oro2	Orokawa SR	20 x 20	1860084	5857345	4
Oro3	Orokawa walkway	20 x 20	1860321	5861411	3
MIPP91	Mayor Island	20 x 20	2798958	6427288	-
MIBT91	Mayor Island	20 x 20	2798709	6427829	-
MITiki91	Mayor Island	20 x 15	2799175	6428022	-
MIPP09	Mayor Island	20 x 20	2798958	6427288	-
MIPP209	Mayor Island	20 x 20	2798962	6427343	-
MITiki09	Mayor Island	20 x 15	2799175	6428022	-
MIBT09	Mayor Island	20 x 20	2798709	6427829	-
PatIs1	Pataua Island SciR	20 x 20	1963729	5782346	4
PatIs2	Pataua Island SciR	20 x 20	1963581	5782639	4
Whale1	Moutohora SR	20 x 20	1950525	5802450	-
Whale2	Moutohora SR	20 x 20	1950837	5802446	-
Whale3	Moutohora SR	20 x 20	1949107	5803267	-
GrtBar1	Great Barrier Island	20 x 20	1823982	5978845	-
GrtBar2	Great Barrier Island	20 x 20	1815275	5986814	-
GrtBar3	Great Barrier Island	20 x 20	1823287	5991198	-
Rab1990	Motuotau	20 x 20	1881886	5830257	2
Rab2011	Motuotau	20 x 20	1881886	5830257	3

Appendix two: Forest survey quadrat site variables. Drainage classes are as follows: (g) good/well drained, (m) moderately drained, (p) poorly drained.

Quadrat name/identifier	Distance from sea (m	Altitude (m asl)	Aspect (°)	Slope (°)	Drainage class	Physiology
Kohi1	64	55	30	60	g	slope
Kohi2	91	40	102	50	g	slope
Kohi3	164	75	293	30–40	g	slope
Kohi4	187	60	100	20	g	face
Kohi5	87	60	-	20–25	g	slope
Oho1	600	70	350	0–5	g	terrace
Oho2	315	40	320	32	g	hill slope
Oho3	1516	150	320	32	m-p	slip scar
Oho4	474	70	270	15	g	slip scar
Oho5	962	130	180	27	g	ridge slope
Oho6	598	60	270	10	g	face
Matata slip	900	40	320	35	g	new slip
Mat1	982	43	300	35	g	ridge slope
Mat2	973	30	310	40	g	slope face
Mat3	723	25	270	45	g	slope face
Mat4	1003	50	45	30–40	m	face
MatS	400	16	232	vertical	g	stream edge
Mater1	657	15	315	0	g	terrace
Mater2	680	40	200	30–35	g	face
Mater3	692	15	0	0	m	terrace
Piko1	318	60	140	25–30	m	slope
OscRev1	1704	75	130	18	m	face
OscRev2	1792	40	270	20	g	ridge slope
Oro1	318	60	100	20–25	g	face
Oro2	60	30	140	15	g	face
Oro3	48	18	180	25	g	ridge slope
MIPP91	97	-	160	5–10	g	-
MIBT91	94	-	215	2	g	-
MITiki91	305	-	135	5–20	g	-
MIPP09	97	-	160	5–10	g	-
MIPP209	160	-	-	-	g	-
MITiki09	305	-	135	5–20	g	-
MIBT09	94	-	215	2	g	-
PatIs1	36	15	325	40	g	face
PatIs2	68	20	225	30–35	g	face
Whale1	40	20	250	5	g	face
Whale2	37	25	135	2	g	terrace
Whale3	60	55	180	5	m	gully
GrtBar1	40	30	110	15	g	face
GrtBar2	110	38	45	10	g	face
GrtBar3	30	20	135	20–30	g	face
Rab1	20	35	-	20	g	crest
Rab2	20	35	-	20	g	crest

Appendix two (continued): Forest survey quadrat site characteristics continued.

Quadrat name/identifier	Ground cover (%)					Canopy height (m)	Emergent height (m)	Canopy Cover (%)
	Litter	Vege-tation	Non vascular	Bare rock	Bare ground			
Kohi1	80	15	-	-	5	20	-	70
Kohi2	70	20	-	-	10	15–17	-	80–90
Kohi3	90	8	2	-	-	10–12	15	65–75
Kohi4	50	40	5	-	5	15	20	80
Kohi5	5	85	5	-	5	15	-	40
Oho1	80	20	-	-	-	20	30	60–70
Oho2	90	10	-	-	-	15	20	70–80
Oho3	70	30	-	-	-	15	20	70–75
Oho4	60	39	1	1	-	17	-	60–70
Oho5	80	25	-	-	5	15–20	20	70
Oho6	40	50	5	-	5	20	25	90
Matata slip	90	10	-	-	-	15–20	-	10
Mat1	90	10	-	-	-	-	-	-
Mat2	70	10.5	5.5	-	10.5	15	-	80
Mat3	30	60	5	-	5	8	14	60
Mat4	30	60	-	5	5	15	17	85
MatS	-	40	-	60	-	0.2	-	-
Mater1	15	50	10	15	10	3	4	50
Mater2	70	15	3	3	4	5	5	-
Mater3	20	30	0	30	20	3	4	30
Piko1	60	20	5	-	15	18–20	-	60–70
OscRev1	70	14	10	2	4	15–20	-	70
OscRev2	66	30	2	10	2	15–20	-	70–80
Oro1	40	45	5	-	10	10–15	-	80–90
Oro2	83	5	2	-	10	15	-	70
Oro3	50	35	5	5	5	15	-	45
MIPP91	-	-	-	-	-	14–16	-	-
MIBT91	-	-	-	-	-	18–20	-	-
MITiki91	-	-	-	-	-	14–16	-	-
MIPP09	-	-	-	-	-	14–16	-	-
MIPP209	-	-	-	-	-	-	-	-
MITiki09	-	-	-	-	-	-	-	-
MIBT09	-	-	-	-	-	18–20	-	-
PatIs1	60	35	-	5	5	15	18	70
PatIs2	50	45	5	-	-	15	18	65
Whale1	70	20	-	10	-	12	12	90
Whale2	55	35	-	10	-	10	14	70
Whale3	60	30	-	10	-	16	16	95
GrtBar1	55	30	1	2	2	18	18	85
GrtBar2	30	60	5	0	5	10–15	20	75
GrtBar3	28	68	2	2	2	7	7	60
Rab1	-	-	-	-	-	-	-	-
Rab2	80	15	1	2	3	18-20	-	75

Appendix three: Species stem density (stems ha^{-1}) of dominant and common species in forest quadrats. Table continues on the following page.

	Beilschmiedia tawa	*Brachyglottis repanda*	*Coprosma lucida*	*Coprosma grandifolia*	*Coprosma macrocarpa*	*Coprosma robusta*	*Coriaria arborea*	*Cordyline australis*	*Corynocarpus laevigatus*	*Cyathea dealbata*	*Cyathea medullaris*	*Dysoxylum spectabile*	*Geniostoma rupestre*
Kohi1	0	100	175	0	0	0	0	0	0	0	0	0	150
Kohi2	0	275	625	0	200	0	0	0	0	0	0	0	100
Kohi3	0	500	650	0	0	0	0	0	0	50	50	0	1100
Kohi4	0	150	200	0	0	600	0	0	0	0	0	0	150
Kohi5	0	200	150	0	0	0	0	25	0	0	0	100	600
Oho1	0	125	1175	0	0	0	0	0	0	150	0	25	550
Oho2	0	1350	1800	25	0	75	0	0	0	25	50	0	2400
Oho3	0	700	850	0	0	0	0	0	0	200	100	0	1300
Oho4	0	167	966	0	0	0	0	0	0	200	0	0	1698
Oho5	50	125	125	0	0	0	0	0	0	100	25	125	125
Oho6	75	50	75	100	0	0	0	0	0	425	0	650	375
Mat1	0	0	225	0	0	75	0	0	0	475	0	0	0
Mat2	0	0	475	0	0	100	0	0	0	175	0	0	100
Mat3	0	0	25	0	0	150	0	0	0	600	125	0	0
Mat4	0	75	25	0	0	75	0	0	0	175	100	0	250
MatT1	0	400	0	0	0	1200	0	0	0	0	0	0	0
MatT2	0	0	0	0	0	1200	2000	0	0	0	0	0	0
MatT3	0	0	0	0	0	800	2000	0	0	0	0	0	0
Pik1	0	50	0	0	0	0	0	0	0	0	200	0	0
OscR1	0	50	25	0	0	25	0	0	25	75	300	25	100
OscR2	0	675	25	0	0	0	0	0	25	300	25	25	0
Oro1	0	975	100	0	250	200	0	0	25	625	125	250	525
Oro2	0	200	0	0	50	125	0	0	0	325	0	0	125
Oro3	0	475	0	0	0	0	0	0	75	250	0	0	75
Pat1	0	475	650	0	0	0	0	0	0	50	175	0	550
Pat2	0	275	750	0	0	25	0	0	0	150	0	0	375
M-PP91	0	0	500	50	1050	0	0	0	0	0	0	0	400
M-BT91	0	0	0	0	1225	0	0	0	0	0	0	0	0
M-Tiki91	0	0	67	0	133	0	0	0	0	0	0	0	0
M-PP109	0	0	1025	0	2150	0	0	0	0	0	0	0	475
M-PP209	0	0	475	0	1125	0	0	0	0	0	0	0	175
M-tiki09	0	0	0	0	867	0	0	0	0	0	0	33	0
M-BT09	0	0	0	25	1150	0	0	0	25	0	0	0	25
Whale1	0	25	0	0	0	0	0	75	0	0	0	0	850
Whale2	0	0	0	0	200	0	0	175	0	0	50	0	1175
Whale3	0	0	0	0	125	0	0	0	0	0	50	0	50
GB1	50	0	0	0	0	0	0	0	0	650	0	300	0
GB2	100	200	0	0	25	0	0	0	0	250	125	50	50
GB3	0	950	0	0	50	75	0	175	0	0	0	0	300
Opape1	0	0	50	0	0	400	0	0	0	0	50	0	250
Opape2	0	50	450	0	0	0	0	0	0	200	50	0	250
Rab-1990	0	0	0	0	0	0	0	0	0	0	0	0	0
Rab-2011	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix three (continued): Species stems density (stems ha^{-1}) of dominant and common species in forest quadrats. Other = *Carmichaelia australis*, *Rhopalostylis sapida*, *Olearia rani*, *Myoporum laetum*, *Melicytus novae-zelandiae*, *Dacrycarpus dacrydioides*, *Carpodetus serratus*, *Coprosma repens*, *Dicksonia squarrosa*, *Entelea arborescens*, *Freycinetia banksii*, *Leptospermum scoparium*, *Leptecophylla juniperina*, *Nothofagus truncata*, *Pittosporum crassifolium*, *Pittosporum umbellatum*, *Alectryon excelsus*, *Beilschmiedia tarairi*, *Dodonaea viscosa*

	Knightia excelsa	*Kunzea ericioides*	*Litsea calicaris*	*Leucopogon fasciculatus*	*Hedycarya arborea*	*Macropiper excelsum*	*Melicytus ramiflorus*	*Metrosideros excelsa*	*Myrsien australis*	*Pseudopanax arboreus*	*Pseudopanax lessonii*	*Vitex lucens*	Other
Kohi1	0	0	0	0	25	0	0	150	0	25	4125	**0**	1200
Kohi2	0	0	75	0	0	0	0	300	0	75	4425	**0**	125
Kohi3	100	0	125	175	350	0	50	525	75	625	325	0	400
Kohi4	50	0	0	100	50	0	0	1250	0	800	250	**0**	300
Kohi5	50	0	275	0	50	0	475	325	100	25	2600	**0**	0
Oho1	50	0	375	0	150	0	375	225	200	25	50	0	275
Oho2	50	50	100	0	25	0	25	300	150	350	175	0	0
Oho3	100	50	50	0	1200	0	350	150	400	50	0	0	300
Oho4	666	67	100	100	233	0	400	200	100	67	0	0	866
Oho5	50	25	150	0	350	25	400	125	4	50	25	0	25
Oho6	0	0	25	0	75	325	375	25	0	25	0	0	125
Mat1	0	125	25	75	150	75	200	75	275	25	0	0	75
Mat2	0	325	0	75	0	0	0	400	375	150	75	0	225
Mat3	0	120	0	100	25	25	400	425	750	75	0	0	25
Mat4	0	300	75	0	100	400	175	175	225	75	0	0	200
MatT1	0	900	0	200	0	0	0	1500	0	900	100	0	1300
MatT2	0	0	0	0	0	0	0	0	0	0	0	0	0
MatT3	0	0	0	0	0	0	0	0	0	0	0	0	0
Pik1	0	0	575	0	50	1475	450	25	0	0	25	50	250
OscR1	0	0	75	0	200	1025	250	25	100	0	50	125	175
OscR2	0	0	100	50	675	250	625	225	275	0	50	25	125
Oro1	0	0	0	75	375	200	600	50	50	175	25	25	100
Oro2	0	0	0	375	325	200	125	50	150	25	1200	0	225
Oro3	50	0	0	50	0	25	125	900	175	0	325	0	0
Pat1	125	150	0	125	200	125	725	150	75	0	0	0	125
Pat2	25	0	0	25	350	275	125	425	100	0	0	0	0
M-PP91	0	0	0	0	0	150	100	800	1125	50	0	0	0
M-BT91	75	0	75	0	50	200	0	375	495	0	25	0	25
M-Tiki91	133	0	33	0	0	67	167	733	2600	0	0	0	33
M-PP109	25	0	0	0	0	700	150	525	1150	175	0	25	50
M-PP209	0	0	50	0	50	125	100	825	3275	25	25	0	0
M-tiki09	100	0	1600	0	100	2033	333	667	1433	200	0	0	100
M-BT09	75	0	775	0	925	1075	175	300	400	50	75	25	0
Whale1	0	0	0	0	0	0	100	2825	0	0	25	0	0
Whale2	0	0	0	0	0	0	650	1075	0	0	0	0	0
Whale3	0	0	0	0	25	25	1825	1100	0	0	0	475	350
GB1	50	150	0	0	25	0	25	25	0	0	0	0	100
GB2	0	200	0	25	0	0	100	25	25	100	0	0	100
GB3	0	250	0	0	0	50	275	1000	0	0	200	0	100
Opape1	25	0	0	0	75	0	0	1150	900	0	325	0	175
Opape2	100	0	0	0	100	0	0	950	900	100	200	0	550
Rab-1990	0	0	0	0	0	0	0	775	0	0	1043	0	2864
Rab-2011	0	0	0	0	0	0	0	675	0	0	1225	0	1500

Appendix four: Basal area (m^2 ha^{-1}) of dominant and common species in forest quadrats. Table continues on the following page.

	Beilschmiedia tawa	*Brachyglottis repanda*	*Coprosma lucida*	*Coprosma grandifolia*	*Coprosma grandifolia*	*Coprosma robusta*	*Corynocarpus laevigatus*	*Cyathea dealbata*	*Cyathea medullaris*	*Dysoxylum spectabile*	*Geniostoma rupestre*	*Knightia excelsa*
Kohi1	0	0.05	0.25	0	0	0	0	0	0	0	0.14	0
Kohi2	0	0.23	0.50	0	0.320658	0	0	0	0	0	0.07	0
Kohi3	0	0.48	0.77	0	0	0	0	1.30	0.48	0	0.99	4.40
Kohi4	0	0.06	0.14	0	0	1.05	0	0	0	0	0.07	0.48
Kohi5	0.04	0.30	0.28	0	0	0	0	0	0	0.11	1.39	2.14
Oho1	0	0.17	2.39	0	0	0	0	2.89	0	0.02	0.74	22.89
Oho2	0	1.32	2.82	0.01	0	0.19	0	0.55	2.06	0	2.58	0.62
Oho3	0	0.66	1.15	0	0	0	0	4.28	0.95	0	0	9.19
Oho4	0	0.11	1.60	0	0	0	0	7.29	0	0	2.16	31.20
Oho5	0	0.20	0.10	0	0	0	0	4.26	0.27	0.38	0.21	8.36
Oho6	0.28	0.08	0.05	0.13	0	0	0	13.47	0	3.24	0.37	0
Mat1	0	0	0.28	0	0	0.17	0	12.22	0	0	0	0
Mat2	0	0	0.60	0	0	0.13	0	3.48	0	0	0.09	0
Mat3	0	0	0.02	0	0	0.82	0	22.28	4.30	0	0	0
Mat4	0	0.17	0.09	0	0	0.14	0	5.90	1.46	0	0.28	0
MatT1	0	0.19	0	0	0	1.02	0	0	0	0	0	0
MatT2	0	0	0	0	0	0.75	0	0	0	0	0	0
MatT3	0	0	0	0	0	0.58	0	0	0	0	0	0
Pik1	0	0.02	0	0	0	0	0	0	6.36	0	0	0
OscR1	6.27	0.13	0.03	0	0	0.06	0.01	2.78	8.82	0.35	0.11	0
OscR2	0	0.60	0.07	0	0	0	0.19	7.93	0.26	0.07	0.56	0
Oro1	0	3.73	0.36	0	0.85	0.84	0.05	18.64	1.29	0.17	0.87	0
Oro2	0	0.23	0	0	0.11	0.70	0	8.25	0	0	0.39	0
Oro3	0	0.76	0	0	0	0	1.95	9.35	0	0	0.13	2.53
Pat1	0	0.35	1.22	0	0	0	0	1.03	5.47	0	1.03	13.60
Pat2	0	0.23	1.60	0	0	0.08	0	7.14	0.01	0	0.47	2.53
M-PP91	0	0	0.22	0.01	0.85	0	0	0	0	0	0.19	0
M-BT91	0	0	0	0	0.63	0	0	0	0	0	0	2.50
M-Tiki91	0	0	0.16	0	0.56	0	0	0	0	0	0	10.79
M-PP109	0	0	0.50	0	2.10	0	0	0	0	0	0.11	0.17
M-PP209	0	0	0.52	0	0.95	0	0	0	0	0	0.20	0
M-tiki09	0	0	0	0	0.28	0	0	0	0	0.03	0	9.37
M-BT09	0	0	0	0.11	1.63	0	0.05	0	0	0	0.01	2.90
Whale1	0	0.04	0	0	0	0	0	0	0	0	1.26	0
Whale2	0	0	0	0	0.40	0	0	0	1.57	0	1.95	0
Whale3	0	0	0	0	1.07	0	0	0	0.72	0	0.05	0
GB1	1.23	0	0	0	0	0	0	10.04	0	13.54	0	0.54
GB2	0.67	0.76	0	0	0.60	0	0	7.33	1.88	0.19	0.04	0
GB3	0	0.65	0	0	0.02	0.30	0	0	0	0	0.22	0
Opape1	0	0	0.09	0	0	0.47	0	0	1.30	0	0.15	1.08
Opape2	0	0.02	0.39	0	0	0	0	7.12	0.66	0	0.29	1.22
Rab-1990	0	0	0	0	0	0	0	0	0	0	0	0
Rab-2011	0	0	0	0	0	0.14	0	0	0	0	0	0

Appendix four (continued): Basal area (m^2 ha^{-1}) of dominant and common species in forest quadrats. Other = *Carmichaelia australis, Rhopalostylis sapida, Olearia rani, Myoporum laetum, Melicytus novae-zelandiae, Dacrycarpus dacrydioides, Carpodetus serratus, Coprosma repens, Dicksonia squarrosa, Entelea arborescens, Freycinetia banksii, Leptospermum scoparium, Leptecophylla juniperina, Nothofagus truncata, Pittosporum crassifolium, Pittosporum umbellatum, Alectryon excelsus, Beilschmiedia tarairi, Dodonaea viscosa*

	Kunzea ericoides	*Litsea calicaris*	*Leucopogon fasciculatus*	*Hedycarya arborea*	*Macropiper excelsum*	*Melicytus ramiflorus*	*Metrosideros excelsa*	*Myrsien australis*	*Pseudopanax lessonii*	*Pseudopanax arboreus*	*Pseudopanax lessonii*	*Vitex lucens*	Other
Kohi1	0	0	0	0.03	0	0	24.89	0	0	0.04	17.69	0	3.76
Kohi2	0	0.07	0	0	0	0	32.03	0	0	0.17	22.44	0	0.46
Kohi3	0	0.17	0.26	0.47	0	0.03	46.17	0.24	0.74	6.17	0.89	0	0.08
Kohi4	1.85	0	0.27	0.09	0	0	39.65	0	0.34	3.87	0.18	0	0.00
Kohi5	0	1.29	0	0.13	0	0.94	89.55	0.19	0	0.15	22.59	0	1.13
Oho1	0	0.75	0	0.36	0	0.46	30.96	0.87	0.55	0.02	0.35	0	0.37
Oho2	0.10	0.09	0	0.01	0.06	0.02	50.71	0.16	1.16	2.42	0.75	0	0.00
Oho3	1.07	1.88	0	2.44	0	0.66	16.19	1.13	0.31	0.57	0	0	0.00
Oho4	0.02	0.39	0.17	0.89	0	1.39	29.58	0.08	0.02	0.03	0	0	0.25
Oho5	1.30	0.12	0	0.67	0.01	2.00	56.25	1.08	0.02	0.04	0.03	0	0.00
Oho6	0	0.01	0	0.28	0.26	3.83	55.75	0	0.71	0.59	0	0	0.00
Mat1	4.78	0.02	0.16	0.55	0.06	0.54	86.71	0.73	0	0.11	0	0	0.00
Mat2	6.66	0	0.46	0	0	0	35.53	1.34	0	0.32	0.06	0	1.33
Mat3	1.91	0	0.20	0.05	0.04	1.46	17.31	5.08	0.23	0.11	0.64	0	0.00
Mat4	12.33	0.43	0	0.09	0.38	1.39	69.74	0.53	1.01	0.20	0	0	0.10
MatT1	1.22	0	0.13	0	0	0	4.15	0	0	0.79	0.07	0	0.03
MatT2	0	0	0	0	0	0	0	0	0	0	0	0	6.50
MatT3	0	0	0	0	0	0	0	0	0	0	0	0	4.56
Pik1	0	10.28	0	10.28	0.03	4.53	25.29	0	0	0	2.30	18.65	3.30
OscR1	0	0.18	0	0.14	1.34	1.31	17.17	0	0	0	0	5.20	0.00
OscR2	0	0.56	0.08	2.33	0.29	1.39	21.19	1.29	0	0	0.22	0.02	0.65
Oro1	0	0	0.18	0.83	0.09	1.41	54.30	0.23	0	1.09	0.08	1.03	0.41
Oro2	0	0	0.56	1.15	0.19	0.25	43.45	0.24	0	0.02	4.79	0	1.78
Oro3	0	0	0.03	0	0.01	1.89	54.10	0.09	0	0	4.03	0	0.00
Pat1	7.31	0	0.54	0.35	0.22	1.28	13.49	0.25	0	0	0	0	0.33
Pat2	0	0	0.02	1.16	0.32	0.11	89.28	0.51	0	0	0	0	0.00
M-PP91	0	0	0	0	0.32	0.63	63.30	5.09	0	0.01	0	0	0.00
M-BT91	0	0.02	0	0.02	0.14	0	93.94	1.41	0	0	0.00	0	0.00
M-Tiki91	0	0.02	0.09	0	0.23	0.58	47.31	8.09	0	0	0	0	0.15
M-PP109	0	0	0	0	0.21	1.30	60.17	2.39	0	0.04	0	0.01	0.35
M-PP209	0	0.01	0	0.02	0.05	0.72	99.05	4.55	0	0.00	0.01	0	0.00
M-tiki09	0	1.30	0	0.04	3.73	1.25	82.56	6.24	0	0.06	0	0	0.15
M-BT09	0	0.55	0	0.94	1.67	0.87	152.31	1.02	0	0.03	0.03	0.09	0.00
Whale1	0	0	0	0	0	0.08	46.33	0	0	0	0.04	0	1.51
Whale2	0	0	0	0	0	0.89	36.36	0	0	0	0	0	1.08
Whale3	0	0	0	0.12	0.01	9.33	24.53	0	0	0	0	9.50	3.59
GB1	8.94	0	0	0.30	0	0.02	77.52	0	0	0	0	0	0.75
GB2	10.57	0	0.03	0	0	0.99	119.79	0.01	0	0.57	0	0	0.06
GB3	0.42	0	0	0	0.03	0.57	17.74	0	0	0	0.12	0	1.95
Opape1	0	0	0	0.05	0	0	40.49	1.95	0.98	0	0.77	0	0.00
Opape2	0	0	0	0.08	0	0	63.31	1.51	0.27	0.16	0.45	0	1.12
Rab-1990	0	0	0	0	0	0	29.47	0	0	0	3.35	0	0.33
Rab-2011	0	0	0	0	0	0	66.96	0	0	0	7.80	0	0.10